An Eye on Numbers:
The Processing of Numerical Information
in the Context of Visual Perception

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1 Summary

The capability of understanding and processing numerical information is a critical skill that allows humans to compare, calculate, judge and remember numbers and numerosities. Without this capability, countless processes in everyday life would be very hard to accomplish. This ranges from simple actions like playing dice to the invention of modern techniques, such as personal computers and satellite-based navigation. Hence, it is important to understand the neural processes underlying the (human) perception of numbers and numerosities. As a contribution to this very complex research field I performed three studies using psychophysical methods and electroencephalography (EEG) with the aim to draw general conclusions on human number perception and the processing of numerical information. In the first two studies, I investigated the effect of *spatial numerical association of response codes* (SNARC). This effect is commonly seen as evidence for the concept of a *mental number line* (MNL), which is a metaphor for the fact, that the human brain organizes numbers on a mentally conceived line with small numbers on the left and large numbers on the right.

In my first study I showed the effector dependence of the SNARC effect, by measuring the SNARC effect for three different effectors: bimanual finger responses, arm pointing responses and saccadic responses. In my second study, I showed that the concept of the mental number line can be extended to a *frontoparallel mental number plane*, where small numbers are represented left and down and large numbers are represented right and up. I achieved this result by investigating the SNARC effect for cardinal axes (horizontal and vertical) and for diagonal axes in one and the same subject. This approach allowed me to conclude that the strength of the SNARC effect on the diagonal axes can be expressed as a linear combination of the strength of the SNARC effect along the two cardinal axes.

In this second study I measured the SNARC effect also regarding two sensory modalities (visual presented Arabic digits and spoken number words). The comparison of the SNARC effect elicited by these two modalities revealed that the strength of the SNARC effect depended on the modality of number presentation. Together with the results of the effector dependency of the SNARC effect from my first study this led me to propose the existence of a distributed “SNARC network” in the human brain. Within the framework of this proposal the SNARC effect is elicited in a *central number stage* (CNS) as a consequence of the interaction between numbers and space in the human brain (e.g. as explicated by the MNL). But in addition, the SNARC effect is further modulated by early, modality dependent processing stages and late, effector dependent processing stages. I hypothesize that these stages modulate the SNARC effect, but not the relationship between numbers and space per se.

My first two studies, explored the SNARC effect, based on abstract numbers represented in the, so-called, *approximate number system* (ANS). In addition to the number processing in the ANS, it is known that the human brain is capable of perceiving very small magnitudes (up to four) immediately, a phenomenon called *subitizing*. Previous studies showed that this perception, although very fast, might be influenced by attentional load (Railo et al., 2008; Olivers & Watson, 2008; Anobile et al., 2012). In my third study, I measured the neural basis of the processing of numerical information non-invasively by means of EEG and used the effect of *visual mismatch negativity* to demonstrate the pre-attentive processing of quantities in the subitizing range. In this experiment, I rapidly presented stimuli, consisting of one, two or three circular patches. To ensure that numerosity was the relevant factor, patches were varied for low-level visual features (luminance vs. individual patch size). While participants were engaged in a difficult visual detection task, changes of the number of patches (standard vs. deviant) were processed pre-attentively. The results of my study provide evidence for the idea that numerosity in this small (subitizing) range is processed pre-attentively.

Taken together, I showed that the mental number line could be extended to a frontoparallel mental number plane and eventually even to a three-dimensional mental number space. I found evidence for the dependence of the SNARC effect on sensory modalities as well as on response effectors, suggesting the existence of a distributed SNARC-brain-network. Finally, I revealed some evidence that number processing of small magnitudes in the subitizing range might be pre-attentive.

1.1 Zusammenfassung

Numerische Information zu verstehen und zu verarbeiten ist eine wichtige Fähigkeit, die es dem Menschen erlaubt, Zahlen und Mengen zu vergleichen, zu berechnen, zu beurteilen und zu erinnern. Ohne diese Fähigkeit wären unzählige Abläufe des Alltags nur sehr schwer möglich. Diese reichen von einfachen Tätigkeiten wie Würfelspielen bis hin zur Weiterentwicklung moderner Techniken wie Computer oder satellitenbasierte Navigation. Daher ist es wichtig, die neuronalen Prozesse, die der menschlichen Zahlenwahrnehmung zugrunde liegen, besser zu verstehen. Als einen Beitrag zu diesem sehr komplexen Forschungsgebiet habe ich mit Hilfe von psychophysikalischen Methoden und Elektroenzephalographie (EEG) drei Studien durchgeführt mit dem Ziel, die menschliche Zahlenwahrnehmung und die Verarbeitung numerischer Information besser zu verstehen. In den ersten beiden Studien untersuchte ich den Effekt der räumlich-numerischen Assoziation von Antworten (englisch: *spatial numerical association of response codes*, abgekürzt: SNARC). Dieser Effekt wird gemeinhin als Beleg für das Konzept des *Mentalen Zahlenstrahls* (englisch: *mental number line*, abgekürzt: MNL) gesehen, der wiederum eine Metapher für die Tatsache darstellt, dass Zahlen im menschlichen Gehirn auf einem mental vorgestellten Strahl organisiert sind, mit kleinen Zahlen auf der linken und großen Zahlen auf der rechten Seite.

In meiner ersten Studie habe ich die Effektorabhängigkeit des SNARC-Effektes nachgewiesen, indem ich den SNARC-Effekt für drei unterschiedliche Antwortarten (Effektoren) gemessen habe: Zweihändige Finger-Antworten, Arm-Zeige-Antworten und sakkadische Antworten. In meiner zweiten Studie habe ich gezeigt, dass das Konzept des Mentalen Zahlenstrahls zu einer frontoparallelen Mentalen Zahlenebene erweitert werden kann, auf der kleine Zahlen links und unten und große Zahlen rechts und oben repräsentiert sind. Dazu habe ich den SNARC-Effekt auf den beiden kardinalen Achsen (horizontal und vertikal), sowie auf den beiden diagonalen Achsen jeweils an denselben Probanden untersucht. Diese Untersuchungsmethode erlaubte es mir zu folgern, dass die Stärke des SNARC-Effektes entlang der diagonalen Achsen als Linearkombination der Stärke des SNARC-Effektes entlang der kardinalen Achsen beschrieben werden kann.

In dieser zweiten Studie habe ich darüber hinaus den SNARC-Effekt auch in zwei verschiedenen sensorischen Modalitäten (visuell präsentierte arabische Ziffern und gesprochene Zahlenwörter) gemessen. Der Vergleich des durch diese beiden Modalitäten erzeugten SNARC-Effektes hat gezeigt, dass die Stärke des SNARC-Effektes auch von der Präsentationsart der Zahlen abhängt. Basierend auf den Ergebnissen meiner ersten beiden Studien habe ich die Existenz eines verteilten „SNARC-Netzwerkes“ im menschlichen Gehirn postuliert. Demzufolge würde der SNARC-Effekt in einem *zentralen Zahlen-Abschnitt* (englisch: *central number stage*, abgekürzt: CNS) als Konsequenz der Verknüpfung von Zahlen und Raum im menschlichen Gehirn (wie z.B. durch den Mentalen Zahlenstrahl beschrieben) erzeugt. Allerdings würde der SNARC-Effekt zusätzlich durch andere, frühe, modalitätsabhängige oder späte, effektorabhängige Verarbeitungsabschnitte moduliert. Ich stelle die Hypothese auf, dass diese Abschnitte zwar den SNARC-Effekt, nicht aber die Verbindung zwischen Zahlen und Raum an sich modulieren.

Meine ersten beiden Studien, die den SNARC-Effekt untersucht haben, basierten auf abstrakten Zahlen, die im sogenannten *Ungefähren Zahlen System* (englisch: *approximate number system*, abgekürzt: ANS) repräsentiert sind. Es ist bekannt, dass zusätzlich zur Zahlenverarbeitung im ANS das menschliche Gehirn fähig ist, sehr kleine Anzahlen (bis zu vier) nahezu instantan wahrzunehmen. Dieses Phänomen wird *Subitizing* genannt. Frühere Studien haben gezeigt, dass, obwohl diese Wahrnehmung sehr schnell ist, sie dennoch durch zusätzliche Aufmerksamkeitsaufgaben beeinflusst werden kann (Railo et al., 2008; Olivers & Watson, 2008; Anobile et al., 2012). In meiner dritten Studie habe ich die neuronale Grundlage der numerischen Informationsverarbeitung nichtinvasiv mittels EEG und einem Effekt, der als *visuelle Mismatch Negativity* bezeichnet wird, untersucht, um herauszufinden, ob die Verarbeitung numerischer Information in diesem Subitizing-Bereich prä-attentiv erfolgt. In meinem Experiment präsentierte ich in schneller Abfolge Stimuli, bestehend aus ein, zwei oder drei Kreisen. Um sicher zu gehen, dass wirklich die Anzahl als relevante Größe verarbeitet wurde, habe ich die Stimuli für niedrigschwellige visuelle Eigenschaften (wie Luminanz und individuelle Kreisgröße) variiert. Während die Probanden mit einer schwierigen visuellen Detektions-Aufgabe beschäftigt waren, wurden Veränderungen in der Anzahl der gezeigten Kreise (Standard oder Abweichung) prä-attentiv verarbeitet. Das Ergebnis meiner Studie bietet einen weiteren Hinweis für die Idee, dass Anzahlen im kleinen (Subitizing-) Bereich tatsächlich prä-attentiv verarbeitet werden.

Zusammengefasst habe ich in meiner Dissertation gezeigt, dass der Mentale Zahlenstrahl zu einer frontoparallelen Zahlenebene erweitert werden kann, möglicherweise sogar zu einem dreidimensionalen Mentalen-Zahlen-Raum. Des Weiteren belegte ich die Abhängigkeit des SNARC-Effektes sowohl von der sensorischen Modalität als auch von der Antwortart, was die Existenz eines verteilten SNARC-Netzwerks im Gehirn nahelegt. Schlussendlich fand ich Hinweise dafür, dass die Verarbeitung von kleinen Anzahlen im Subitizing-Bereich prä-attentiv sein könnte.

2 Introduction

Numbers and numerosities are essential to life. In daily routine we often count items, for example, when we go shopping: *How many bananas do I have in my trolley?* We use numbers to sort, assign and remember things: *The office is on the third floor, room number 314.* We use numbers to compare things: *Which is the leading football team?* We can calculate with numbers to get answers to important questions: *Can I afford this car, when I get a 10% discount?* Numbers are involved in virtually everything we use every day, for instance, computers, clocks, planes, telephones and banking transactions. Most of science, education, engineering and economy would be rendered impossible to accomplish without numbers. All these examples show the importance of numbers to our life and hence indicate the significance to understand how numbers and numerosities are processed in the human brain. In my thesis I investigated the brain processes underlying number perception and processing with methods of psychophysics and electroencephalography. In the following I will give a detailed introduction to the terms *number* and *numerosity*. Afterwards I will summarize some basic features of vision and visual perception, followed by a short description of the neuroscientific method of electroencephalography (EEG). Finally, I will introduce the concept of mismatch negativity.

2.1 Numbers and Numerosity

In this section I will give a detailed introduction on number perception and the neuronal processes underlying numerical processing. I will start by reviewing number processing in the human brain and I will introduce the reader to three currently known "number systems", models that stand for the neural and/or behavioural handling of different number magnitudes. I will then proceed with discussing the effects on number perception that are relevant for this thesis, with special focus on the effect of the spatial numerical association of response codes (SNARC). Following these discussions, I will introduce the concept of a mental number line (MNL). Finally, I will present the basic physiological principles on number processing in human and animal brains.

2.1.1 The Three Senses of Number

For a long time, it was argued that humans (and maybe some animals too) use two distinct non-symbolic number systems (see Feigenson et al., 2004 for a review), but recent research has suggested that rather three instead of two systems might determine the human number processing (see Anobile et al., 2016 for a review). These three systems differ in the range of represented and processed numbers (see Figure 2-1). For small amounts of items, humans do not need to count, but can immediately tell their number. This behavioural phenomenon is called *subitizing* and is supposed to be handled by the *object tracking system* (OTS) (Trick & Pylyshyn, 1994; Feigenson et al., 2002). For larger amounts of items, human beings use an *approximate number system* (ANS), and when the number exceeds a certain threshold, the *texture density system* (TDS) replaces the ANS and hu-

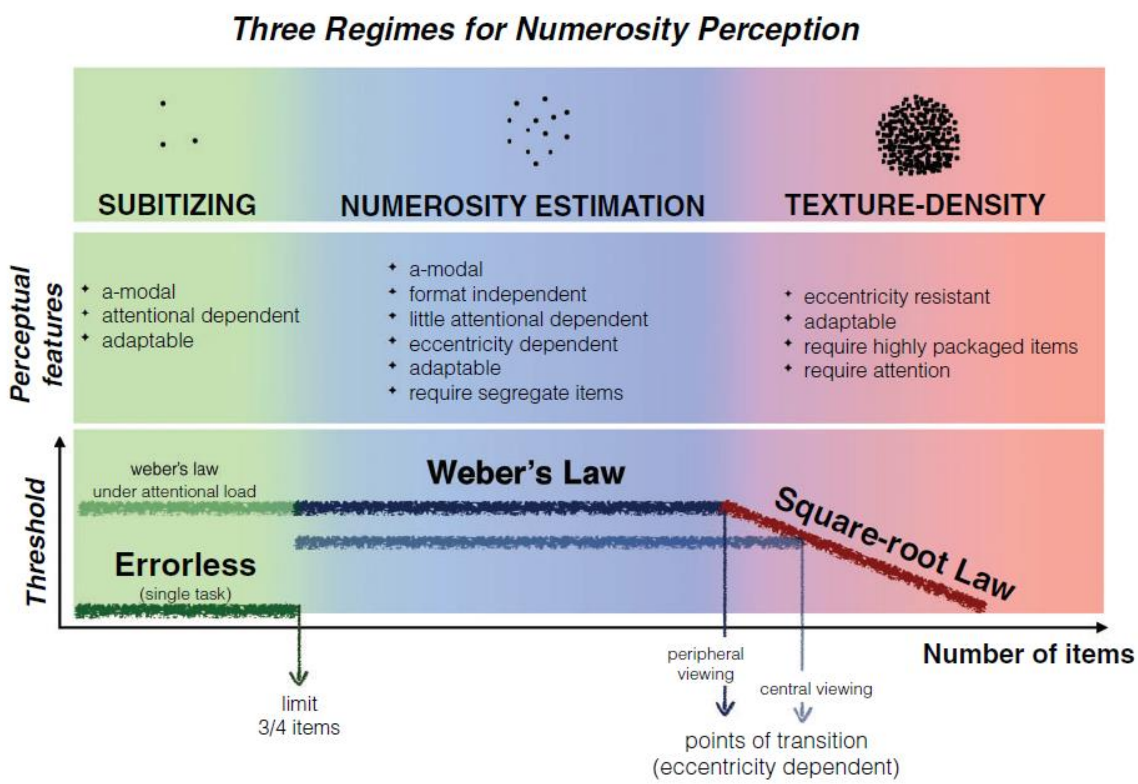


Figure 2-1: Schema of the proposed three distinct regimes of number perception. *Subitizing*, coloured in green, is most likely handled by the *object tracking system* (OTS) and processes small numerosities. Larger numbers of items are processed by the *approximate number system* (ANS), coloured in blue. For many items in a small area, the *texture density system* (TDS), coloured in red, takes over. (Modified from Anobile et al., 2016)

mans rather judge the texture than the exact magnitude. In the following chapters I will introduce these three distinct number systems.

2.1.1.1 The Object Tracking System (OTS)

Humans immediately recognize the amount of very few items (up to four) without counting (Mandler & Shebo, 1982). This phenomenon is called *subitizing*, from the Latin word *subitus*, meaning *sudden* and it has been reported also for animals, for example, for rhesus macaques (Hauser & Hauser, 2000). It has been proposed that subitizing is performed in an *object tracking system* (OTS) that keeps track of a small number of items by assigning markers to each item individually (Trick & Pylyshyn, 1994; Feigenson et al., 2002). The limitation in the subitizing range is hypothesized to be a result of a limitation of available markers and hence a limit of trackable objects. The subitizing range increases to up to four items during the early life-span. As shown by Starkey and Copper (1980), young infants up to the age of two managed to choose the larger amount of objects when choosing between 1 and 2 or 1 and 3 crackers, but failed when the amounts were 3 and 6 or even 1 and 4. Since 4 and 6 were both beyond their subitizing range, the infants were unable to decide to their advantage.

Subitizing is not restricted to visual perception, but was also found for auditory (Camos & Tillmann, 2008) and haptic stimuli (e.g. Plaisier et al., 2009). Based on the processing speed in such tasks, subitizing was assumed to be pre-attentive (Trick & Pylyshyn, 1993, 1994; Pylyshyn, 2001), i.e. to emerge without voluntary or involuntary attention paid to the perceived stimulus. A recent study by Anobile and colleagues (2012), however, showed that subitizing, in contrast to numerosity estimation, was influenced by attentional load. In this study, subjects had to enumerate a cloud of dots or to locate the position of the number of dots in this cloud on a number line. Participants' performance decreased when they were simultaneously engaged in an auditory, visual or haptic memory task. Based on these results, Anobile and colleagues (2016) suggested that subitizing may reflect the operation of attentive mechanisms. Such mechanisms are known to have a very limited capacity (Burr et al., 2010b). Furthermore, they argued that this system may "sit on top" of the ANS, supporting the estimation of this system for low numbers.

2.1.1.2 The Approximate Number System (ANS)

Stimuli with a magnitude larger than four are not processed by the OTS anymore, when counting is prevented, for example, with high presentation frequency (e.g. Wahlen et al., 1999). Since an exact tracking of every item is impossible (Feigenson et al., 2002), subjects seem to estimate the number of items with their so-called *approximate number system* (ANS). In adult humans, but probably also in other animals, as reported for monkeys (Brannnon & Terrace, 2002) and recently for crows (Ditz & Nieder, 2016), this estimation is not equally exact for each number. The just noticeable difference between number pairs increases with increasing magnitude of the number pairs, thereby obeying the Weber-Fechner law (Moyer & Landauer, 1967). The Weber-Fechner law is a universal rule in perception, stating that the noticeable change of a stimulus feature *p* scales logarithmic with the total stimulus feature magnitude *S* and the constant parameter *k* that depends on the exact experimental settings:

$$p = k \cdot \ln S \tag{1}$$

The result of this logarithmic compression is a ratio-dependency for discrimination of two magnitudes within the processing range of ANS. This ratio is rather large for young infants and decreases across the life span to a certain level. For example, six-month-old infants can discriminate magnitude ratios of 1 : 2 but not of 2 : 3 (Xu & Spelke, 2000). Older children and adults are capable of discriminating much smaller ratios (e.g. 7 : 8), even between different sensory modalities, such as visual point arrays and visual or auditory sequences (Barth et al., 2003; Agrillo et al., 2015).

Another characteristic of the ANS is that stimulus magnitudes are adaptable. When a sequence of single points was presented to a participant with a low frequency, resulting in a small number of stimuli, the amount of following test stimuli presented at the same frequency was overestimated. In contrast, a rapid presentation, resulting in a large number of stimuli, led to an underestimation of the test stimulus amount. Remarkably, adaptation was not dependent on the sensory modality of the stimuli. Adaptation also occurred for auditory stimuli and even cross-modally, i.e. auditory stimuli influenced the perceived amount of visual stimuli and vice versa (Arrighi et al., 2014). This cross-modal adaptation was considered evidence for an amodal-number-sense and for the idea that numerosity perception can be completely unrelated to texture perception (Anobile et al., 2016). Further support for this hypothesis arose from a study by He and colleagues (2009). These authors reported the dependence of number perception from clouds of dots, when dots were connected by lines. Dots were either connected to pairs, triplets or were unconnected. When dots were connected (e.g. twelve dots pairwise to six pairs), a fewer amount of dots was perceived (e.g. ten) especially for short presentation times. Anobile and colleagues (2016) claimed that this result indicates that connected dots were partially perceived as single object. Since the numerosity perception was influenced by the connections, although the total amount of dots did not change, this might indicate a difference between numerosity and texture density.

2.1.1.3 Texture Density System (TDS)

Among others, this example (see previous section) from He and colleagues (2009) led Anobile and colleagues (2016) to the assumption that along with the OTS and the ANS a third number system must contribute to the human number sense. They proposed that this third number system is *texture density* based and comes into play for very large amounts of stimuli within a small area. This is similar to the visual *crowding* phenomenon, when single objects are packed too close together to be distinguishable from each other. Anobile and colleagues (2014) showed that for such large amounts of stimuli the Weber fraction was not constant (see e.g. Dehaene, 2011), but decreased proportionally with the square root of numerosity after a critical point. Furthermore, Anobile and colleagues (2015) showed that the transition between numerosity processed by the ANS and the *texture density system* (TDS) depended on the eccentricity of the displayed stimuli: the more eccentric the stimuli were presented, the earlier the TDS took over. This is plausible since visual resolution is poorer in the periphery than close to the fovea. Another prediction resulting from these results was that, like for crowding, the transition between the ANS and the TDS should depend on the centre-to-centre spacing of the stimuli, rather than the edge-to-edge distance (see Levi, 2008 for a review). This has been confirmed by Anobile and colleagues (2015), too.

2.1.2 Abstract Number Processing

So far I mostly reported on number processing in humans based on magnitudes and quantities. But aside from that, humans are also capable of converting (approximate) magnitudes in abstract numbers and vice versa (see Dehaene, 1992 for a review). This is especially important for mathematical operations, such as addition, subtraction, multiplication and division, but also for parity judgments. Thereby, the abstract number representation in the human brain might be activated by written or spoken number words and digits (McCloskey et al., 1991; but see Dehaene, 1992). This concept of abstract numbers is probably learnt (in school) and hence culturally dependent. Surveys and studies on aborigines, who did not come into very close contact with (western) culture, showed that even though no *number words* were used by them, they still had an intuitive understanding of numerosity despite the fact they were poor in counting higher magnitudes (Gordon, 2004; Dehaene et al., 2008). In the following I will report some psychological effects (partially) based on the abstract number concept.

2.1.2.1 The SNARC Effect

Many studies have shown that in the human brain numbers and perception of space are strongly linked. One of the most popular findings in this vein is that humans link small numbers with the left-hand side and large numbers with the right-hand side of space. The earliest report on this link has been made by Dehaene and colleagues (1990), who showed that participants, when judging the magnitude of a two-digit number, were faster with left-hand reactions to small numbers and right-hand reactions to large numbers. This effect was also present when participants had to judge parity (see Figure 2-2) of the numbers instead of magnitude (Dehaene et al., 1993) and was termed the *SNARC effect* (abbr. for: <u>s</u>patial <u>n</u>umerical <u>a</u>ssociation of <u>r</u>esponse <u>c</u>odes). Given that in a parity judgement task participants did not have to “compute” the magnitude of a number explicitly, but still showed an effect of response side, the SNARC effect has been considered unequivocal evidence for the link between numbers and space.

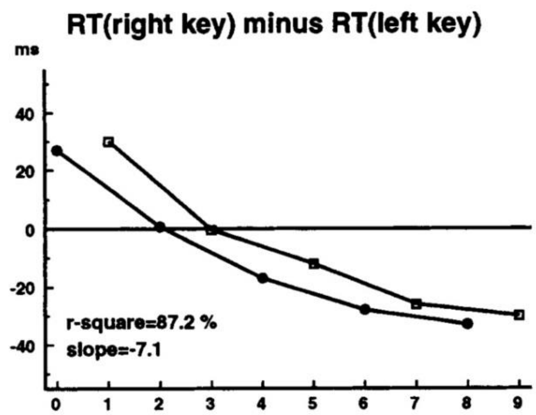


Figure 2-2: First demonstration of the SNARC effect. Response time differences (answer with right hand minus answer with left hand) plotted over presented numbers. Negative slope of response time differences indicates a SNARC effect. (Modified from Dehaene et al., 1993)

Since the discovery of the SNARC effect numerous follow-up studies were performed. The SNARC effect has been reported for highly diverse stimulus categories: Arabic digits, written number words, dice pattern, spoken number words (Nuerk et al., 2005) or Chinese digits (Kopiske et al., 2015; but see Hung et al., 2008). Based on these results, the SNARC effect was postulated to be amodal, i.e. independent from the presentation modality of the number (Nuerk et al., 2005). This amodality of the SNARC effect has been challenged by Wood and colleagues (2006b) who did not find a significant correlation between results from auditory stimulus presentation mode and any of the three other tested visual stimulus presentation modes (Arabic digits, written number words, dice pattern).

The SNARC effect has been demonstrated for numerous different effectors such as bimanual responses (e.g. Dehaene et al., 1993), unimanual pointing responses (e.g. Fischer, 2003; Bingel & Heath, 2011), saccadic eye movements (e.g. Schwarz & Keus, 2004), pedal responses (e.g. Schwarz & Müller, 2006), grip movements (Andres et al., 2004) and vocal responses (Leth-Steensen & Citta, 2016). The SNARC effect has also been reported for answers given with index and middle finger of the same (right) hand (Priftis et al., 2006). Interestingly, the orientation of the hand (prone or supine) had an influence on the SNARC effect. A SNARC effect was found when the orientation of the hand was in line with the mental number line (MNL), i.e. participants with prone right hand or supine left hand showed a SNARC effect (Riello & Rusconi, 2011).

Over time, many modulatory factors on the SNARC effect have been reported. For example, the reading and writing direction influenced or even reversed the SNARC effect (Deahene et al., 1993). Additionally, finger counting habits showed an influence on the SNARC effect (Fischer, 2008). Participants who started counting with their left hand (around 2/3 of a subject group) showed a significant SNARC effect, while the “right hand starters” showed no significant SNARC effect. Sex has an influence on the SNARC effect, too. Male subjects showed a significant stronger SNARC effect than female subjects (Bull et al., 2013).

In addition to reaction time, a SNARC effect has also been revealed for response accuracy: participants answered more likely wrong for large numbers, if the requested response direction was left and vice versa (Schwarz & Keus, 2004; Keus & Schwarz, 2005; Nuerk et al., 2005; but see Wood et al., 2006a).

Interestingly, orientation of the SNARC effect has not only been shown for the horizontal axis (e.g. Dehaene et al., 1993), but also for the vertical axis in a frontoparallel plane with bi- and uni-manual button presses (Ito & Hatta, 2004; Gevers et al., 2006a; Shaki & Fischer, 2012; Holmes & Lourenco, 2011, 2012; Hartmann et al., 2014) and saccadic eye movements (Schwarz & Keus, 2004). In these studies, the vertical axis appeared to be oriented in a way that western subjects reacted faster to small numbers at the bottom and large numbers at the top (but see Hung et al., 2008 for Chinese subjects). Experiments performed by Ito and Hatta (2004), Gevers and colleagues (2006a) and Shaki and Fischer (2012) used response buttons that were mounted in the sagittal and not in the vertical orientation. Accordingly, it might have been the case that these experiments demonstrated a SNARC effect in depth (along the sagittal axis) rather than along the vertical axis (see Winter et al., 2015 for a detailed discussion on this issue). Hartmann and colleagues (2014) used button presses along the vertical axis and reported a significant vertical SNARC effect. Interestingly, no vertical SNARC effect was found when responses were given with one hand and one foot (Hartmann et al., 2014, Exp. 2 - 4). In contrast to these findings, Holmes and Lourenco (2011, 2012) reported a significant vertical SNARC effect only in “primed” participants: Participants showed the vertical SNARC effect when exposed to priming of numerical vertical magnitude (levels of a building or water height in a pool) but not when exposed to priming of numerical order (items on a shopping list). Holmes & Lourenco argued that there might in fact be no spontaneous vertical number orientation at all. In addition to the studies listed above the SNARC effect in depth has also been shown by Chen and colleagues (2015). In this study, the answers along the sagittal axis to “near” positions were executed faster for small numbers and answers to “far” positions were executed faster for large numbers.

Concerning reproducibility, the SNARC effect was found to have a comparably high inter-subject variability. Several studies reported an occurrence of the SNARC effect in around two thirds of the participants (Nuerk et al., 2004; Riello & Rusconi, 2011; Wood et al., 2006a; Viarouge et al., 2014b). Based on studies on number-synaesthetes, it has been argued, that this variability of the SNARC effect might be due to individual differences in implicit mental representation of numbers (Cohen Kadosh & Henik, 2007), differing from the left-to-right representation proposed by Dehaene and colleagues (1993). Interestingly the strength of the SNARC effect has been found to correlate significantly with the amount of grey matter in a subregion of the human posterior parietal cortex, implying a stationarity of the SNARC effect within participants over time (Krause et al., 2014).

Another factor known to have an influence on the SNARC effect is age. Early studies did not find a SNARC in children below the age of nine years, i.e. three years of schooling (Berch et al., 1999). These authors reasoned that young children do not implicitly know about the parity of a number, but need to “compute” it each time. When getting older, the knowledge about parity of numbers gets more implicit and is additionally influenced by the MARC effect (Berch et al., 1999; see chapter 2.1.2.2 The MARC Effect). More recent studies (Hoffmann et al., 2013) reported that children aged five and a half years indeed did not display a SNARC effect when judging magnitude, but exhibited it when judging the colour of a number. Since judgement of colour, just like parity judgment, does not require a processing of number magnitude, this has been taken as further evidence that reading and writing habits alone cannot explain the SNARC effect.

As reviewed above, the SNARC effect is widely accepted as evidence for a link between numbers and space in the human brain. A common interpretation is that, at least in western culture, humans organize numbers along a *mental number line* (MNL), where small numbers are located more to the left and large numbers are located more to the right (Dehaene et al., 1993). This MNL interpretation is consistent with the number line learned in school.

In addition to the MNL, another possible explanation, named the *polarity correspondence principle* (PCP), could account for the association of number and space, as revealed by the SNARC effect (Proctor & Cho, 2006; see Winter et al., 2015, section 3.5 for a review). The PCP is based on the observation that many binary classifications are asymmetrical in a way that one of the two classifications is more general than the other (e.g. awake or asleep). These more general classifications are seen as *[+] polar* while the opposite is seen as *[–] polar*. A "response advantage" (lower reaction times or more precision) is assumed when the polarity of the stimulus dimension and the polarity of the response dimension correspond. The PCP is strongly linked to the linguistic concept of *markedness*. Linguistically, some words are considered as "unmarked" while other words are considered as "marked" (see chapter 2.1.2.2 The MARC Effect for a detailed explanation of *markedness*). The PCP assumes that large numbers as well as unmarked words are [+] polar while small numbers as well as marked words are [–] polar. Since "right", "up" and "far" are considered as unmarked and hence [+] polar and "left", "down" and "near" are considered as [–] polar (c.f. Winter et al., 2015), the PCP account could explain a SNARC effect in all three spatial dimensions. However recent studies (e.g. Fischer & Shaki, 2016) showed a SNARC effect even with centrally presented stimuli and centrally given responses. Additionally, the SNARC effect did not occur for vocal answers "bad" ([–] polar) and "good" ([+] polar), while it occurred for answers "left" and "right" (Leth-Steensen & Citta, 2016). Both effects cannot be explained by the PCP but support the concept of a MNL.

2.1.2.2 The MARC Effect

Another robust spatial-numerical compatibility phenomenon is the MARC (linguistic markedness of response codes) effect (Nuerk et al., 2004). It describes the phenomenon that, when judging parity with the left and right hand, participants react faster for odd numbers on the left hand and for even numbers on the right hand. Nuerk and colleagues (2004) argued that this effect relies on the *linguistic markedness* of words. It is well known that within a given language, the frequency of the occurrence of certain words differs considerably (c.f. Roettger & Domahs, 2015). For example, the word "true" appears more often in the English language than the word "untrue". In linguistic context the word "true" would be considered as unmarked while the word "untrue" would be considered as marked. In general, unmarked words represent the more universal case while marked words are more specific. In some cases, markedness is expressed with a prefix (e.g. "un-" or "in-"). Since odd and left are both linguistically marked while even and right are linguistically unmarked, it was suggested that participants experience a speed benefit when markedness is congruent. Alternatively, the MARC effect could be explained by the *polarity correspondence principle* (PCP, see also chapter 2.1.2.1 The SNARC Effect - polarity correspondence principle), if one would assume that odd and left are both coded as [–] polar, while even and right are coded as [+] polar (Cho & Proctor, 2007). This latter explanation was further supported by findings that the MARC effect relies on handedness: it is reversed for left-handers (Huber et al., 2015). This result cannot be explained purely in linguistic terms.

2.1.2.3 Other Effects on Number Processing

Along with the SNARC effect and the MARC effect, other effects on number processing have been described. Since these effects are not central to my dissertation project, I will present them only briefly. The *numerical distance effect* (Moyer & Landauer, 1967; Dehaene et al., 1990) describes the phenomenon, that participants, when being asked to judge the relative magnitude of two numbers, are slower and less accurate when the two numbers are closer together (e.g. 2 and 3) than when the two numbers are more separated (e.g. 2 and 7). The distance effect was also obtained, when numerical magnitude was irrelevant (Dehaene & Akhavein, 1995). It is commonly seen as further evidence for the existence of a *mental number line* (MNL), with the idea, that compared numbers are mentally searched on the MNL and the closer together the two numbers are, the harder is it to separate them from each other.

Number comparison is also influenced by the *numerical size effect* (e.g. Svenson, 1975), also called *numerical magnitude effect*. This effect describes the phenomenon that for the same numerical distance, numbers of higher magnitude are harder to distinguish than numbers of lower magnitude. For instance, it is considered to be more easy to judge whether 1 is smaller or larger than 3 than whether 76 is smaller or larger than 78. The size effect is in line with Weber's law (c.f. equation (1) in chapter 2.1.1.2 The Approximate Number System (ANS)) and is commonly interpreted as evidence for the logarithmic scaling of the MNL (e.g. Nuerk et al., 2001) at least for higher magnitudes (see also e.g. Verguts & Van Opstal, 2005 for a review on this two effects).

It is still under debate whether the *mental number line* (MNL) is mapped in a logarithmic or linear fashion. For instance, Nuerk and colleagues (2001) proposed a logarithmic representation of numbers on the MNL. In contrast, Fischer and Campens (2009) presented evidence that at least small numbers are mapped in a linear way. Since all these studies were performed with participants grown up in western culture and (probably) exposed to intensive mathematical education in school, an impact of cultural interference cannot be excluded. In a study with Amazonian indigenes, who were not exposed to this kind of education, participants showed a logarithmic MNL. In contrast, western control subjects showed a linear MNL in most cases. Only in conditions with high numbers (up to 100), which prevented counting, western subjects displayed a logarithmic MNL, too (Dehaene et al., 2008). This led to the assumption that the linear MNL, while present in western subjects, is an achievement of cultural, mathematical education and the "original" mapping of number is logarithmic.

2.1.3 Neuronal Basis of Number Perception

A large body of studies investigated the neuronal basis of number perception and processing in the human brain. A convergent series of results has localised the *approximate number system* (ANS) bilaterally in the horizontal segment of the intraparietal sulcus (hIPS). This brain region is recruited in numerous number processes, such as number comparison (e.g. Chochon et al., 1999) or mental arithmetic (e.g. Dehaene et al., 1999; Menon et al., 2000; Simon et al., 2002). Furthermore, the hIPS has been identified as the source of the *numerical size effect* and the *numerical distance effect* (Dehaene, 1996; Pinel et al., 2001; see chapter 2.1.2.3 Other Effects on Number Processing). A hIPS activation has been reported for nonverbal numerical visual symbols or auditory stimuli (Eger et al., 2003), for sets of items (Piazza et al., 2003) or number words (Pinel et al., 2001), even when participants were not aware of the number presentation (Naccache & Dehaene, 2001). These findings are in line with findings reported from neurological patients. For example, the case of a patient with a small left parietal lesion has been reported. This patient had a wide-ranging deficit in number processing. Only the numbers one to four were still processed (Cipolotti et al., 1991). Other studies showed comparable number processing restrictions for patients with a lesion in hIPS (e.g. Dehaene & Cohen, 1997). These patients were not capable of simple arithmetic. This deficit was independent of the presentation modality and the response type. Also in the IPS, but apart from the hIPS in the *inferior IPS*, a component of the *object tracking system* (OTS) has been located (Xu & Chun, 2006; Xu, 2009). The authors have shown that this area is one of the stages in visual object processing. When presenting objects to participants, a fixed number of up to four objects is selected based on their spatial location (see markers hypothesis in chapter 2.1.1.1 The Object Tracking System (OTS)) in the inferior IPS, while other object features, such as shape, are encoded in other areas (superior IPS and lateral occipital complex) .

In *functional magnetic resonance imaging* (fMRI) experiments the ratio between objects (dot amount and line length) was adapted, so that *blood-oxygen-level dependent* (BOLD) activity was decreased for a certain ratio. When a deviant ratio was presented, the BOLD response to the deviant ratio was increased compared to the BOLD response to the adapted ratio. Results demonstrated domain-specific coding of magnitude ratios in the anterior intraparietal sulcus (Piazza et al., 2004; Jacob & Nieder, 2009). No selective activation in areas such as the primary visual cortex (V1) has been reported in these studies, since the stimuli were controlled for low-level-features, such as luminance, density and size. Additionally, it has been reported that the human IPS has a columnar organization for number (similar to the columnar organization for oriental tuning in V1). In this study, participants were exposed to diverse clouds of dots or objects. To achieve a purely magnitude based effect, stimuli were controlled for total area, dot size, circumference and density (Harvey et al., 2013).

Additionally to hIPS, fMRI studies revealed two other brain areas to be engaged in number processing: the left angular gyrus (AG) and the posterior superior parietal lobe (PSPL) bilaterally (see Figure 2-3). The angular gyrus was activated when tasks required verbal processing of numbers (Dehaene et al., 1999). Dehaene and colleagues (2003) proposed that the AG as part of the language system would contribute to the number processing only if strong demands on verbal coding of numbers were required. An example for this would be multiplication (Chochon et al., 1999), since the “basic multiplications” are not computed but stored in verbal memory, e.g. as multiplication tables (Dehaene, 2011). This proposal was further supported by a lesion-study where a patient (with lesions in the IPS) lost conceptual knowledge of arithmetic, but was still capable of simple memory based calculations, such as multiplications, some additions and subtractions (Delazer & Benke, 1997).

Activity in PSPL was found to be enhanced during number approximation (Dehaene et al., 1999), number comparison (Pinel et al., 2001) and counting (Piazza et al., 2002). The PSPL is known to be unspecific to number processing, but also plays a role in other actions, such as reaching, grasping or working memory and has a role in selection of mental dimensions such as time and space (Coull & Nobre, 1998; Wojciulik & Kanwisher, 1999). Dehaene and colleagues (2003) suggested that the PSPL could additionally contribute to attentional selection of numbers. This attentional selection would, for example, play a

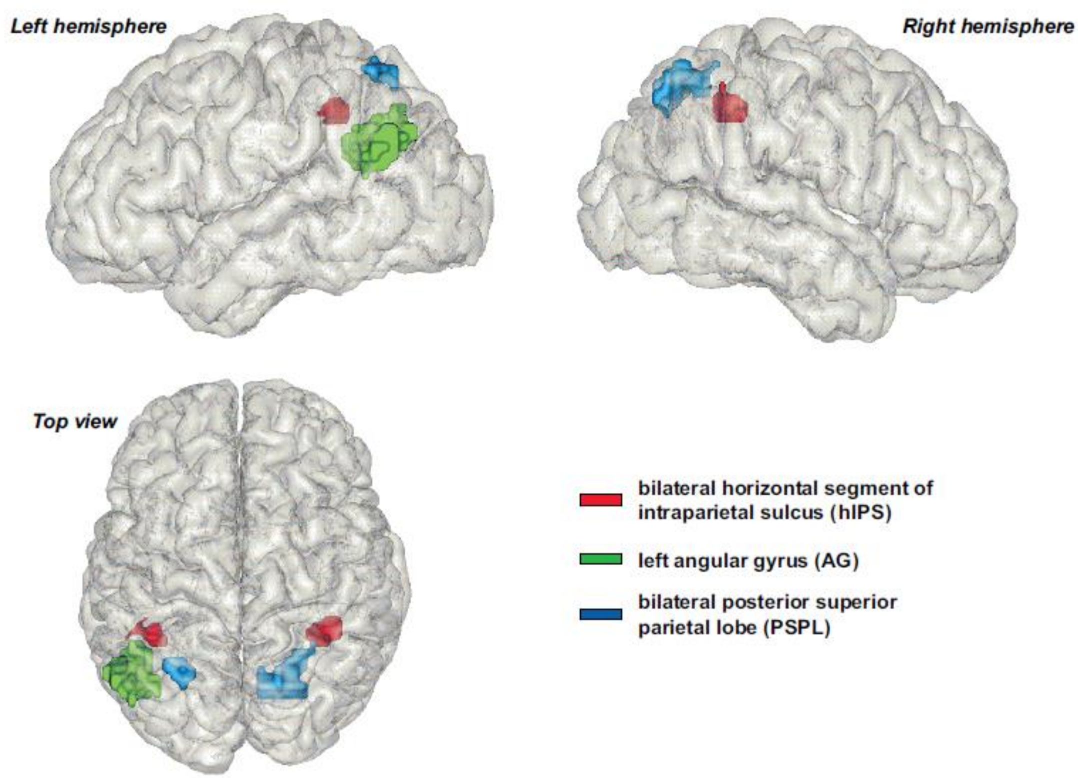


Figure 2-3: A Human brain model (Talairach) with areas highlighted that are involved in number processing. Only voxels that showed activity in at least 40% of several analysed studies are coloured in this schema. Three brain areas are distinguished: (i) Bilateral the horizontal segment of intraparietal sulcus (hIPS) is coloured in red, (ii) the left angular gyrus (AG) is coloured in green and (iii) bilateral the posterior superior parietal lobe (PSPL) is coloured in blue. (Modified from Dehaene et al., 2003)

role, when judging which of two quantities is larger (Pinel et al., 2001) and would also rely on the link between numbers and space (see also chapter 2.1.2.1 The SNARC Effect).

Even at the level of individual neurons number processing can be observed. Nieder and colleagues (2002, 2006) and Nieder and Miller (2004) reported the existence of neurons tuned for number processing in monkeys' *intraparietal sulcus* (IPS) and *lateral prefrontal cortex* (PFC). These neurons even responded when stimuli were presented sequentially over time for both, visual and auditory stimuli (Nieder, 2012). In these studies, monkeys were trained to judge the numerosity of a cloud of dots or a sequence of dots flashed over time relative to a control stimulus. The magnitude range up to five items was tested and neurons tuned for these magnitudes were found. Sequential and simultaneous presentations activated different subsets of neurons, suggesting that different populations of neurons were involved in numerosity extraction from serial and parallel presentation. Some neurons in PFC and the *ventral intraparietal area* (VIP) were activated by auditory and visual numerosity (Nieder, 2012) for the same magnitude, hence encoding a number of items independently from the sensory modality. These findings could be confirmed even for monkeys that were never trained for numerosity discrimination (Viswanathan & Nieder, 2013). Interestingly, and in line with findings on numerosity, sensory-modality-independent encoding of spatial information has been found in macaque area VIP (Schlack et al., 2005). A functional equivalent of macaque area VIP has been found in the human parietal cortex (Bremmer et al., 2001). In addition to magnitude, the length of bar-stimuli has also been found to activate neurons in the IPS, interestingly in an area that was functionally overlapping with magnitude coding (Tudusciuc & Nieder, 2007) and number related responses (Simon et al., 2002). Besides these findings in the area VIP, number selective neurons were also reported in the neighbouring *lateral intraparietal area* (LIP) (Nieder & Miller, 2004; Roitman et al., 2007). These neurons responded to numerosity in a rather monotonic fashion, with an increase in the firing rate with increasing stimulus amount, in contrast to neurons in VIP, where certain neurons fire for certain numerical values. Among other characteristics, neural activity in area LIP can reflect intention to perform a saccade (see Snyder et al., 2000 for a review). This functional overlap of number information processing and saccade planning might be another indicator for an evolutionary link between numbers and space. Functional equivalents of macaque area LIP have been identified in humans IPS (e.g. Konen et al., 2004; Konen & Kastner, 2008; Kleiser et al., 2009).

2.1.3.1 Functional Coupling of Numbers and Saccades

In addition to the link between numbers and space (see concept of MNL in chapter 2.1.2.1 The SNARC Effect) support for a functional coupling between numbers, space and saccades has been presented by Burr and colleagues (2010a) and Binda and colleagues (2011). Experimental results provided evidence that during saccades not only space and time, but also number perception was modulated. In the experiments, participants were instructed to compare the magnitude of elements in a cloud of random dots briefly flashed before, during, or after a saccade. About 50 ms around saccade onset the perceived magnitude was significantly decreased. In a follow-up study, by Binda, Morrone and Bremmer, participants underestimated the outcome of a rapid mental arithmetic calculation (addition and subtraction) when operands were displayed briefly before a saccade onset (Binda et al., 2012). Another link between saccades and arithmetic has been reported by Knops and colleagues (2009). The authors trained a multivariate classifier algorithm to identify the direction of a saccadic eye movement (left or right) based on fMRI data. Remarkably, this left and right classification algorithm could be employed to distinguish within the same subjects between addition and subtraction calculations. The addition calculations were "classified" as rightward saccades, while subtractions were associated with leftward saccades. This is in congruence with the concept of the *mental number line* (MNL), since on such a line subtractions correspond to movements to the left (e.g. 10 – 3 = 7; seven is on the left side of ten on the MNL), while additions correspond to movements to the right.

2.2 Structure of the Visual System and Eye Movements

Humans perceive the world through different senses. In primates, the most important sensory modality is *vision.* In the following I first describe the physiological basis of visual perception. Then I shall present an overview on eye movements, followed up by a more detailed discussion of a specific class of them, the saccades. Finally, I shall introduce the eye tracking method I used in my studies.

2.2.1 Visual Pathways

Visual information processing starts in the eyes. Light waves reflected by the environment travel through the dioptrical apparatus of the eye and eventually reach the retina. Here, photons are absorbed by two different types of photoreceptors, rods and cones, and translated into receptor potentials. Cone density is highest in a retinal region forming the fovea. Following the photoreceptors, visual information is processed by different retinal cell classes: bipolar, horizontal, amacrine and ganglion cells. Ganglion cell axons leave the eye and send visual signals towards central processing stages (Dudel et al., 2001; Purves et al., 2004). The most important pathway for conscious visual perception is the retinothalamo-cortical pathway, comprising the retina, the *lateral geniculate nucleus* (LGN), and the *primary visual cortex* (V1), which is located in the *occipital lobe* (Purves et al., 2004). Starting from here, visual information processing is subdivided into two visual pathways, a *ventral stream* and a *dorsal stream*. This functional dichotomy has been deduced from studies in neurological patients (see Goodale & Milner, 1992 for a review), but also from neurophysiological recordings in the animal model, i.e. the macaque monkey (Mishkin & Ungerleider, 1982). The *ventral stream* (or so-called “what pathway”) is important for object identification and recognition whereas the *dorsal stream* (or so-called “how or where pathway”) is involved in encoding of position and motion information. A schema of the visual cortical system of the animal model is shown in Figure 2-4. Areas in both pathways are not strictly separated and share many connections between each other (Felleman & Van Essen, 1991). Numerous studies of the last two decades have revealed similarities of the processing of visual information in the human and the monkey brain. Bremmer and

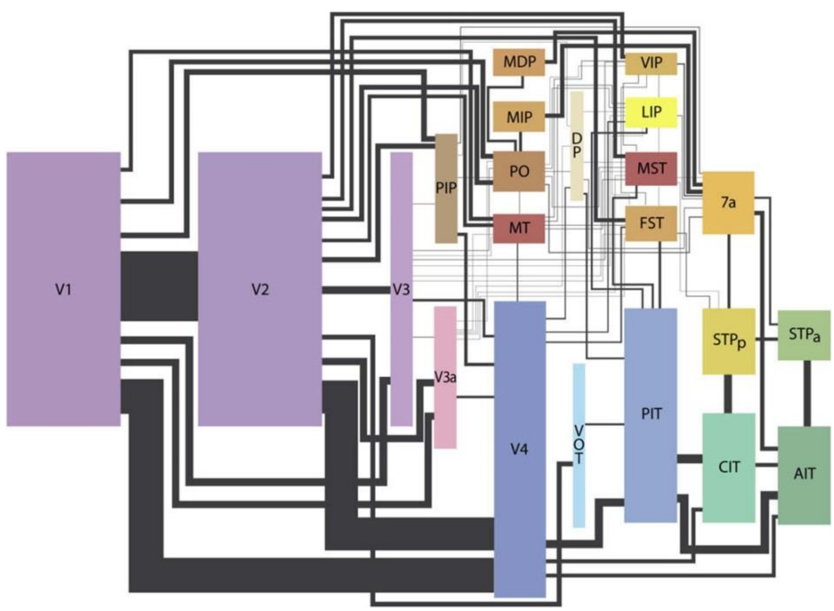


Figure 2-4: Schema of Macaques’ brain areas involved in vision. Coloured rectangles represent visual brain areas. Size of the rectangles is proportional to the cortical surface of the corresponding area. Grey bands represent connections between areas and have a thickness proportional to the estimated number of fibers in the connection. Areas related to the dorsal stream are drawn above the equator of the figure (coloured in reds and browns), while areas related to the ventral stream are drawn below the equator of the figure (coloured in blues and greens). Processing complexity increases from left to right. (Wallisch & Movshon, 2008)

colleagues (2001), as an example, found strong evidence for the existence of a functional equivalent of monkeys' area VIP in the human *intraparietal sulcus* (IPS). Furthermore, a functional equivalent of monkeys' area LIP has been identified in the humans' IPS (e.g. Heide et al., 2001; Konen et al., 2004, 2007; Konen & Kastner, 2008; Kleiser et al., 2009).

2.2.2 Eye Movements

Since the fovea forms the area with the spatial highest resolution of the retina, primates need to move their eyes to bring or keep objects of interest in the fovea. In human vision six different classes of eye movements are distinguished, grouped in foveating and reflexive eye movements (see Carpenter, 1988; Leigh & Zee, 2006 for a review). The reflexive eye movements are the *vestibular-ocular reflex* (VOR) and the *optokinetic nystagmus* (OKN), both responsible for stabilizing visual perception (Ilg, 1997). The VOR stabilizes the visual perception during head movements by counter-movements of the eye (Aw et al., 1996). The OKN is induced by large field image motion on the retina (e.g. Lappe & Hoffmann, 2000). The group of foveating eye movements consists of *smooth pursuit eye movements* (SPEM), *vergence*, *fixation* and *saccades*. SPEMs are employed to keep moving points, items or areas on the fovea (e.g. Robinson, 1965). *Vergence* specifies the movements of the two eyes in opposite directions to change the focus between different spatial depths. *Fixational* eye movements (tremor, drifts and microsaccades) occur during fixation of objects, points or areas. It is generally assumed that these tiny eye movements (with amplitudes of only a few minutes of arc) aim to prevent vision from fading out (e.g. Martinez-Conde et al., 2004). Finally, *saccades* are very fast eye movements that change eye position to different parts of the visual field. Since saccades are of specific interest to my thesis, I describe them in more detail in the following chapter.

2.2.2.1 Saccades

Saccades are rapid eye movements that are used to bring an object of interest onto the fovea. On average, saccades are performed about three times per second (Rayner, 1998; Land, 1999), which is more frequent than the human heart beat. Saccades can be executed to visual, auditory, tactile and even invisible (remembered or imaginary) targets.

Saccades are *ballistic* eye movements, i.e. once initiated they cannot be aborted and have a stereotyped velocity profile (Carpenter, 1988).

The relation between saccade amplitude and peak velocity is described by the saccadic *main sequence* (named after astronomical classification of stars). For small amplitudes up to 15° of visual angle the relation is linear (Bahill et al., 1975). For greater amplitudes peak velocity shows a slight saturation. Saccadic peak velocity can reach values of 450°/s and more. Like peak velocity, saccade duration scales with saccade amplitude. Saccades with amplitudes of 5° typically last between 20 ms and 30 ms. Each additional degree of visual angle in saccadic amplitude increases the duration by roughly 2 ms. Saccadic latency, i.e. the time from an event triggering a saccade until its onset, changes with different experimental conditions. For visually guided saccades, humans show a mean saccadic latency of roughly 200 ms, with a wide range from 120 ms up to 350 ms (Carpenter, 1988; Leigh & Zee, 2006).

2.2.2.2 Eye Tracking

Human eye movements can be recorded in many different ways. Today video based eye trackers such as the *Eyelink 1000* system (SR Research Ltd., Ottawa, Canada) are gold standard. Such systems emit (invisible) infrared light. This infrared light falls through the pupil and is absorbed within the eye, but reflected by the participant's iris, conjunctiva, etc. These different reflection and absorption behaviours allow for online detection of the pupil. After a calibration, during which subjects have to fixate a number of target points at known positions on the setup screen, the eye-tracking-system can calculate the participant's gaze position on the screen from the participant's pupil position. The position of the eye is determined from fitting an ellipsoid to the pupil. Such infrared eye tracking is very precise (average accuracy: 0.5° of visual angle) and has a high temporal resolution (500 Hz and 1000 Hz with the systems used for the experiments described in my thesis).

2.3 Electroencephalography (EEG)

Among many other scientific techniques such as functional magnetic resonance imaging (fMRI) or neurophysiological recordings, *electroencephalography* (EEG) is an established method for measuring brain activity. EEG on humans has been first performed in 1929 by Hans Berger, who reported that he could measure the activity of the human brain by placing electrodes on the scalp (Berger, 1929). In EEG-measurements the amplitude of the voltage difference between two electrodes is typically plotted over time. EEG can be used to record spontaneous electrical activity in the brain (e.g. for clinical diagnostics). In basic research, EEG signals are often related to stimulus or event on- or offsets and recorded as *event-related potential* (ERP) (for details see chapter 2.3.4 Event-Related Potentials (ERPs)), as it is common in neuroscience. At first I explain the physiological principles underlying EEG measurements in this chapter. This is followed up by a description of the applied setup hardware and a short outline concerning frequency components in EEG (EEG bands). In the end, I will explain the two analysis methods used in my thesis, *event-related potentials* and *time-frequency-analysis*, in detail.

2.3.1 Physiological Background

The physiological basis of EEG-signals is well known (see Luck, 2005 for a review). When an excitatory neurotransmitter is released at the apical dendrite of a cortical pyramid cell, positive current from the extracellular space flows into the cell. This results in an overall negativity outside of the cell in the region of the apical dendrite (see Figure 2-5 A). The region around the cell body is positively charged, relative to the negatively charged region at the apical dendrite. These two regions (negative dendrite region and positive cell body) act as a physical dipole along the neuron and produce an electric field. When a neuron receives an inhibitory instead of an excitatory signal the resulting dipole of the neuron is reversed.

The dipole of a single neuron is too weak to be measured at the scalp surface, but when several (some thousands to many millions) neurons are activated at approximately the same time the electric fields sum up under certain conditions (see Figure 2-5 B). The resulting electric fields induce electrical current changes on the skull (see Figure 2-5 C), which can be measured as voltage changes with electrodes attached to the scalp. For this summation of electric fields, it is important that the single neurons are spatially aligned and not randomly orientated, because in this case the electric fields would cancel out. This is also true for two neighbouring neurons receiving inhibitory and excitatory signals. Since the brain's surface is not flat, but folded in so-called sulci, it is also possible that two groups of neurons on opposite sides of a sulcus cancel each other's electric field out. One problem in EEG measurements is that a dipole can elicit voltage changes even in electrodes far away from its position. Hence, voltage changes in EEG electrodes at a certain position do not necessarily imply brain activity at this position in the brain.

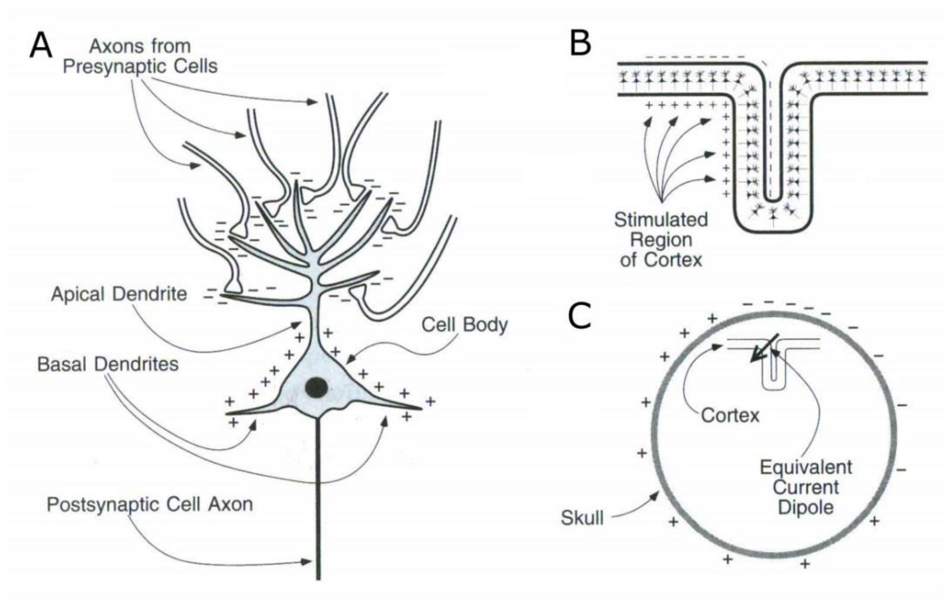


Figure 2-5: Schema of physiological principles underlying EEG measurements. An electrical dipole is formed as reaction of neurotransmitter release at the apical dendrite of a pyramid cell neuron (A). Several neuronal dipoles combine to a larger dipole (B). A large dipole elicits a current change on skull (C). (Modified from Luck, 2005)

2.3.2 Hardware Setup

In my thesis, I measured EEG signals using 64 active (amplifying) electrodes that were fixated on an electrode cap. Spatial arrangement of the electrodes (see Figure 2-6) followed the *extended international 10 - 20 system* that ensures comparable electrode positions across experiments and studies. "10 - 20" thereby refers to the fact that the distance between neighbouring electrodes is either 10% or 20% of the total left-right (from ear to ear) and front-back (from *nasion* to *inion*) distance on the skull (c.f. Jasper, 1958, figure 1; Odom et al., 2010, figure 1). Since I used the *extended* system in my thesis, the distance between electrodes was always 10%. The large number of electrodes allowed for a high density measurement of the EEG. The 10 - 20 system also unifies the naming of the electrodes. Each electrode is labelled with a letter and a number. Thereby the letters *F* (frontal), *T* (temporal), *P* (parietal) and *O* (occipital) refer to the adjacent cortical lobe. For convenience the letter *C* (central) is used for the central scalp region. The hemisphere location is coded by numbers. Odd numbers (1, 3, 5 and 7) refer to the left hemisphere while even numbers (2, 4, 6 and 8) refer to the right hemisphere. The letter “z” (for zero) denotes electrodes in the midline between the two hemispheres (c.f. Jasper, 1958; Odom et al., 2010). In addition to the 64 electrodes a 65th electrode, named *ground* (*Gnd*), was attached to the middle of the forehead (position *FPz*). This special electrode “grounds” the

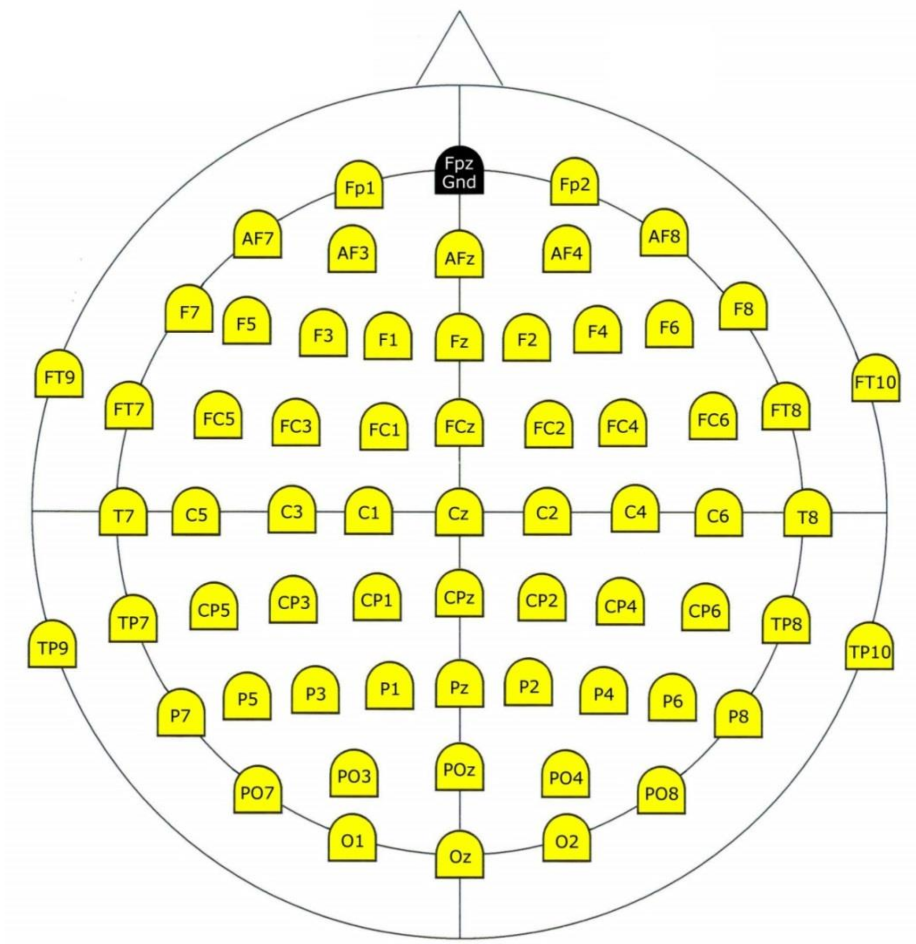


Figure 2-6: Schema of the electrode distribution on the scalp according to the extended international 10 - 20 system. The upper side of the schema corresponds to the participant’s forehead and the lower side to its back of the head. (Modified from Brain Products GmbH, Gilching, Germany)

participant's body to reduce global changes in electrical charge and hence improves the signal to noise ratio in EEG signals (e.g. Luck, 2005). In my experiment, voltage changes on electrodes were at first recorded with respect to the reference electrode (*Cz* in my setup) with a sample frequency of 1000 Hz. In a subsequent analysis, I re-referenced the recorded signals to the sum of electrodes *TP9* and *TP10*. These electrodes are located behind the ears where, in my experiment, no or only rare experiment related brain activity was assumed (c.f. Luck, 2005).

2.3.3 Frequency Components

With and without sensory input and no matter whether participants are awake or asleep some neurons in the human brain are "active" and induce electrical dipoles, as explained before. The activity of the neurons oscillates, which can be recorded by means of EEG. Oscillations are typically categorized by their oscillation frequency in so-called frequency "bands" (see Stothart & Kazanina, 2013 and Herrmann et al., 2014 for a review). Frequencies below 4 Hz comprise the so-called *delta band*, those between 4 Hz and 8 Hz the so-called *theta band*. Frequencies between 8 Hz and 12 Hz (or up to 14 Hz) comprise the so-called *alpha band*. Higher frequencies are subdivided in the so-called *beta band* (up to 30 Hz) and the *gamma band* (above 30 Hz). The activity in certain frequency bands is sometimes indicative of specific behavioural conditions: high activity in the alpha band is known to reflect a relaxed mental condition, while activity in the gamma band is increased, when participants perform voluntary movements or sensory-motor tasks (Buzsáki, 2011). Furthermore, selective attention processes and distractor suppression have been associated with alpha oscillation (Foxe & Snyder, 2011) while gamma and theta band oscillation have been linked to visual working memory (Tallon-Baudry et al., 1998; Tallon-Baudry & Bertrand, 1999; Rizzuto et al., 2003).

2.3.4 Event-Related Potentials (ERPs)

As mentioned above a common way to use EEG in neuroscience is to analyse *event-related potentials* (ERPs). In such an analysis, the continuously recorded data is aligned to an event (e.g. visual stimulus appearance, start of a sound or a button press) and sliced, i.e. cut in short time sequences. These resulting slices contain ERPs elicited by a single event. The noise in the signal is reduced and thereby the signal-to-noise ratio is improved by frequent repetitions of conditions within the same participant and by averaging the recorded ERPs. Oscillatory activity (see chapter 2.3.3 Frequency Bands) cancels out, if oscillations are not precisely linked to event-times. In the following, I will concentrate on the description of ERP components that are elicited by flashed visual stimuli, and omit evoked potentials from other kinds of stimuli (e.g. auditory signals) as they are not important for my thesis.

When a visual stimulus is presented (e. g. briefly flashed) to a subject, *visually evoked potentials* (VEPs) can be recorded as EEG signal (see Luck, 2005 for a review). These VEPs differ depending on the stimulus presentation method (e.g. shortly flashed, continuously presented or moved). In the following, I will focus on VEPs elicited by flashed stimuli, as I only used this kind of stimulus presentation in my thesis. VEPs consist of different components (peaks in the measured voltage). Components are commonly named after their polarity N (negative), P (positive) or C (varying between positive and negative) and additionally enumerated in order of their appearance (e.g. P1). Unfortunately, the enumeration is not generalized and varies across publications. The enumeration I introduce in the following will further be used in the entire thesis (see Figure 2-7).

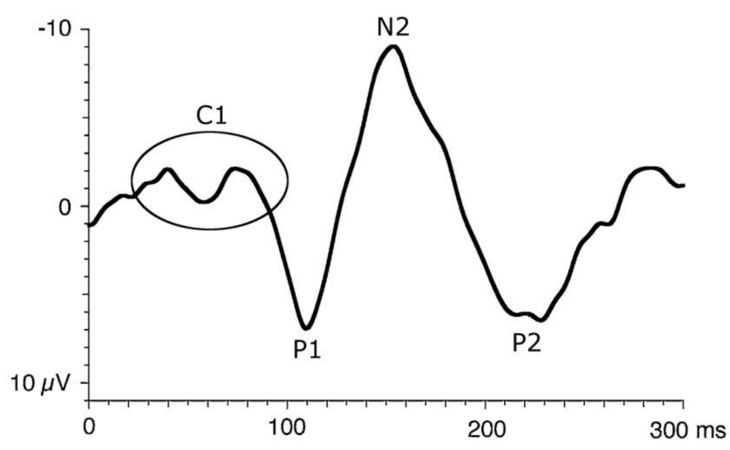


Figure 2-7: Typical VEP as response to a flashed visual stimulus. The voltage signal of an occipital electrode is plotted over time relative to stimulus onset. VEP-components, as described in the text, are marked with respective labels. (Modified from Odom et al., 2010)

The first VEP-component is called C1. The onset of the C1 component is typically around 40 ms to 60 ms after stimulus onset and its peak around 80 ms to 100 ms. The C1 component probably arises in the primary visual cortex (V1) and is negative for stimuli presented in the upper visual field and positive for stimuli presented in the lower visual field (Di Russo et al., 2001; Clark et al., 1995).

The P1 component is typically elicited between 60 ms and 90 ms and reaches its peak at around 100 ms to 130 ms after stimulus onset. Hence, the P1 component often overlaps with the C1 component. It was argued that the early parts of the P1 component arise from the dorsal extrastriate cortex and the later part arises from more ventrally located activity in the fusiform gyrus (Di Russo et al., 2001). The P1 component is known to be sensitive to spatial attention and might reflect a suppression of processing at ignored locations (Hillyard et al., 1998).

The next component is the N2 that typically peaks around 150 ms to 200 ms after stimulus onset on the posterior electrodes and might have a source in the parietal lobe (Di Russo et al., 2001). The N2 component has been shown to be modulated by spatial attention (Hillyard et al., 1998) and is assumed to reflect voluntary discrimination processing (e.g. Hopf et al., 2002). The N2 component varies with stimulus deviance which evokes the so-called *mismatch negativity* (see chapter 2.4 Mismatch Negativity (MMN)). Accordingly, it is central to my thesis.

The last two components, which are of importance for my thesis, are, on the one hand the P2 component that follows the N2 component, and on the other hand, the P3 component. The P2 is commonly found at anterior and central electrodes in a time window between 200 ms to 300 ms. The amplitude of the P2 is known to be modulated by stimulus features: infrequent stimuli with “simple” stimulus features tend to increase the P2 amplitude (Luck & Hillyard, 1994). The P3 component (not shown in Figure 2-7), sometimes also called *P300* for historical reasons due to its peak latency (300 ms to 700 ms), is assumed to be elicited in the frontal lobe and the temporal parietal area (see Huang et al., 2015 for a review) and might be linked to working memory (e.g. McCarthy et al., 1997).

2.3.5 Time-Frequency-Analysis (TFA)

As stated above, the ERP-analysis is based on the averaging of ERPs from different trials and results in temporal alignment of EEG potentials relative to an external event. With this method, noise and oscillatory activity, that is not synchronized with the stimulus, are cancelled out, since positive peaks in one trial may superimpose with negative peaks in another trial (see Figure 2-8 A and B). One way to investigate oscillations in EEG is to perform a frequency analysis, typically with a fast Fourier transformation (FFT). In the results of such a FFT, frequencies of prominent oscillation can easily be detected in the so-called "frequency domain".

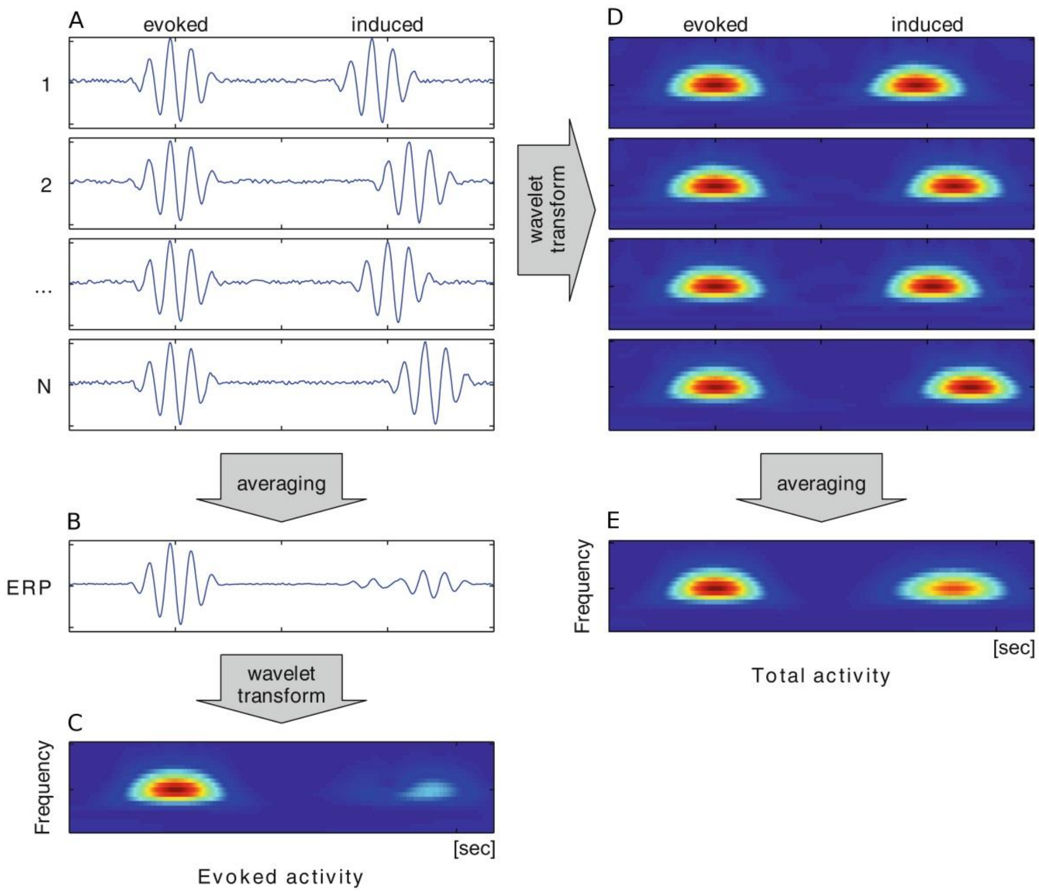


Figure 2-8: Schema of differences between time-frequency-analysis (TFA) performed on singled trials (A) and on averaged ERP (B). TFA based on averaged ERP shows *evoked* (stimulus locked) responses only (C). TFA based on single trials (D) contains the *total activity* including *invoked* (varying with phase from trial to trial) activity (E). (Modified from Herrmann et al., 2014)

Unfortunately, when inspecting EEG data in the frequency domain, the temporal information of the EEG signal cannot be investigated simultaneously at any possible resolution. A way to cope with this problem is a *time-frequency-analysis* (TFA), an analysis typically based on *wavelet transforms* (see Herrmann et al., 2014 for a review). In this analysis, the ERP is convoluted with a wavelet of one central frequency and limited bandwidth around this frequency (see Figure 2-9 A and B). The result of this convolution is plotted over time. This procedure is repeated for different frequencies and results in *time-frequency-plots* (TFPs), which reveal the temporal evolution of spectral components (see Figure 2-9 C and D). The proper adjustment of the wavelets is critical to the outcome of the analysis. Short wavelets with only a few cycles gain a higher temporal resolution than longer wavelets. In contrast, the frequency resolution gets better for longer wavelets. Hence, the proper choice of the wavelet width is a trade-off between time and frequency resolution.

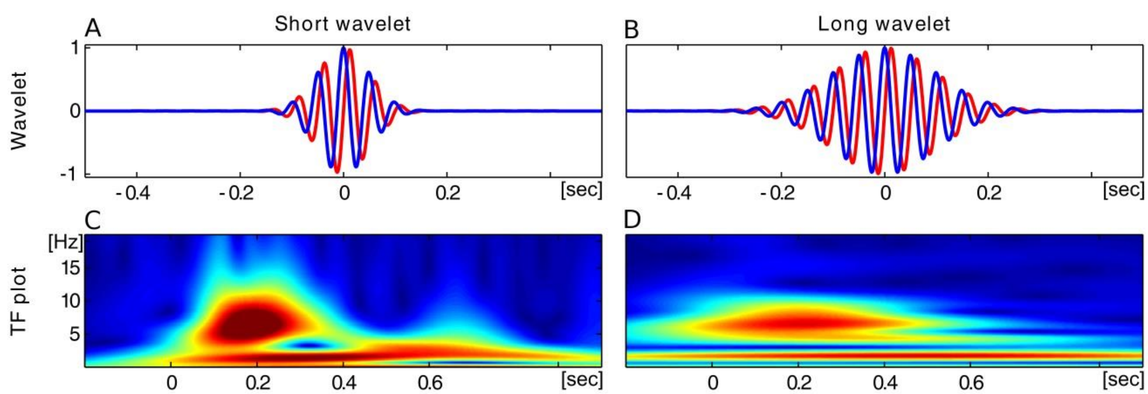


Figure 2-9: Schema of time and frequency resolution of time-frequency-analysis based on wavelet transforms on example data. EEG data is convoluted with a complex wavelet (A and B). Short wavelets (A) result in a higher time resolution (C) while longer wavelets (B) result in a higher frequency resolution (D). (Modified from Herrmann et al., 2014)

TFAs can be applied to averaged ERPs (e.g. within one condition of one participant) or to single trial data. Since in the average of the ERP all *event-related oscillations* (EROs), which were not stimulus locked, are cancelled out, the result of the TFA resembles the ERP-analysis and shows pure evoked responses. In contrast, a TFA based on single trial data results in purely positive TFPs. Hence, by averaging these TFPs no EROs can cancel out and the resultant TFPs contain information of evoked and induced (from EROs varying in phase from trial to trial) responses. This latter approach allows analysing *total activity* (see Figure 2-8) (Herrmann et al., 2014).

2.4 Mismatch Negativity (MMN)

An extensively studied phenomenon in EEG measurements is the so-called *mismatch negativity* (MMN), which describes the effect that ERPs differ, when within a sequence of equal stimuli (called standards) a deviant stimulus occurs. Usually the N2-component (see chapter 2.3.4 Event-Related Potentials (ERPs)), occurring in a time window between 100 ms and 250 ms after stimulus onset, evoked by the deviant stimulus is more negative than the amplitude elicited by the standard stimulus. It is common to illustrate this incongruence by presenting the difference between deviant ERP and standard ERP (see Figure 2-10). Since this difference is negative the effect is called *mismatch negativity*. In a *time-frequency-analysis* (TFA) (see chapter 2.3.5 Time-Frequency-Analysis (TFA)), the deviant stimulus evokes a stronger *event-related oscillation* in the theta band (4 Hz to 8 Hz) than the standard stimulus (Herrmann et al., 2014). I start my description of MMN with an introduction of the, historically first discovered, auditory MMN, followed by a description of the visual MMN. Finally, some possible explanations of the neural processes underlying the visual MMN are presented.

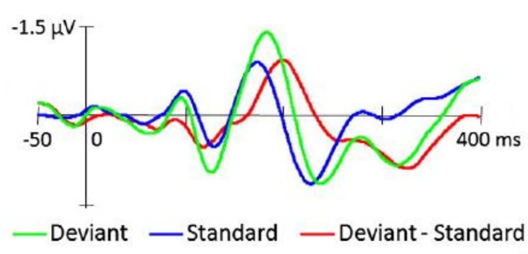


Figure 2-10: Example of mismatch negativity (MMN). ERPs elicited by deviant stimuli are plotted in green, elicited by standard stimuli in blue and difference between ERPs from deviant and standard data in red. MMN occurs in this example between 150 ms and 250 ms. (Modified from Qian et al., 2014)

2.4.1 Auditory Mismatch Negativity

The *mismatch negativity* (MMN) was first revealed for auditory stimuli by Näätänen and colleagues (1978). They presented tones to participants, who had to count one of the stimuli (called deviant stimulus) silently. Deviant stimuli differed either in loudness (experiment 1) or in frequency (experiment 2) from standard stimuli. Näätänen and colleagues reported robust differences in the N2 amplitude (around 175 ms after stimulus onset). For auditory stimuli, a MMN has been demonstrated for a variety of stimulus features, such as loudness, frequency (e.g. Näätänen et al., 1978), duration (e.g. Jacobson & Schröger, 2003) and recently for numerosity (Ruusuvirta & Astikainen, 2016). In this latter study, six tones were presented sequentially consisting of two types of tones, differing in frequency (for simplicity termed A and B). The proportion (or ratio) between tones with frequency A and frequency B was changed in deviant trials (1 : 5 or 2 : 4) compared to standard trials (proportion 3 : 3). Since a MMN does not only occur when participants attend to the deviant stimulus, but also when they are engaged in a difficult task which draws their attention away from standard and deviant stimuli (see Sussman, 2007 for a review), the MMN is commonly seen as evidence for pre-attentive auditory change detection. In the auditory domain, the MMN is found particularly at central and fronto-central scalp electrodes (Näätänen et al., 2007).

2.4.2 Visual Mismatch Negativity

The MMN has not only been demonstrated for auditory but also for visual stimuli (see Kimura, 2012 for a review). The source of the *visual mismatch negativity* (vMMN) has been localized in right-hemisphere occipital visual extrastriate areas and right hemisphere medial prefrontal areas (Kimura et al., 2010a, see Figure 2-11) with a peak in ERP-difference between 150 ms and 400 ms (Kimura, 2012). It has been shown that a task drawing attention to the deviant stimulus (for example, to detect the deviant stimulus) results in a larger MMN (Khodanovich et al., 2010). Furthermore, an interaction between the vMMN and the task has been reported: task related reaction times increased and vMMN amplitude decreased when the target of the task and the deviant stimulus had the same relevant feature (e.g. colour or orientation) (Czigler & Sulykos, 2010). Regardless of the specific experimental paradigms, standard stimuli typically are presented in 80% of the cases and deviant stimuli in 20% of the cases, leading to an *oddball ratio* of 1 : 4 (Kimura et al., 2009).

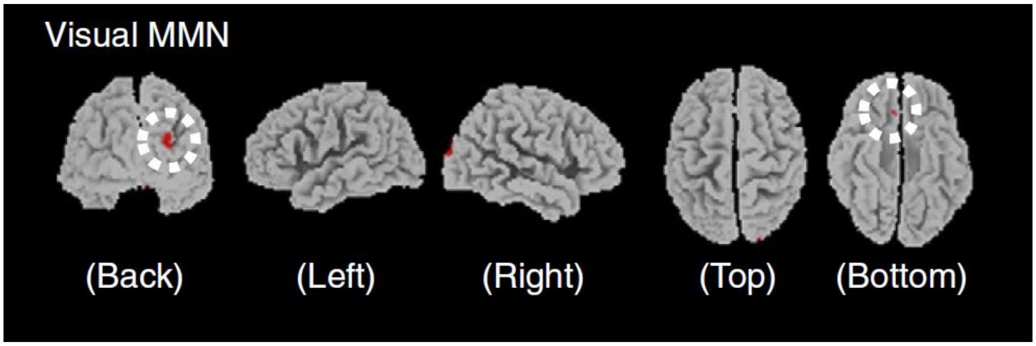


Figure 2-11: Source location of the main generators of visual MMN in the right occipital visual extrastriate areas and the right medial prefrontal areas of the human brain. (Modified from Kimura, 2012)

The visual MMN has been reported for a broad spectrum of visual stimulus features, such as orientation (e.g. Astikainen et al., 2008; Czigler & Sulykos, 2010; Kimura et al., 2010b), size (e.g. Kimura et al., 2008a), location (e.g. Berti, 2009), shape (e.g. Bubrovszky & Thomas, 2011), colour (e.g. Czigler & Sulykos, 2010; Müller et al., 2010), luminance/contrast (e.g. Kimura et al., 2008b), direction of motion (e.g. Pazo-Alvarez et al., 2004; Amenedo et al., 2007), duration (e.g. Qiu et al., 2011), spatial frequency (e.g. Kenemans et al., 2003) and facial expression (e.g. Zhao & Li, 2006).

2.4.3 Neural Processes Underlying Visual Mismatch Negativity

In recent years, different ideas concerning the neural basis of the vMMN have been proposed (see Kimura, 2012 for a review). One possible explanation is that the vMMN reflects memory-mismatch responses. This *memory-mismatch account* assumes that a vMMN is elicited when the presented visual stimulus is incongruent to the memory representation created by the preceding stimuli (Näätänen, 1992). Over the years, this account has been adopted for different ideas concerning the kind of memory representation that is involved in generating vMMN. Possible memory representations could be the *iconic memory*, the *sensory memory* or a *regularity-representation*. According to the *iconic memory variant of memory-mismatch account* the vMMN is elicited when the deviant stimulus is incongruent with the iconic memory of the directly preceding stimulus. This account has been disproved, however, since the vMMN is explicitly dependent on the sparseness of the deviant stimulus (Kimura et al., 2006), while the *iconic memory variant* assumes a vMMN for each change of stimulus regardless of the sparseness of the “deviant” stimulus.

The fact that the vMMN depends on the sparseness of the deviant stimulus is incorporated in the *sensory-memory-trace variant of the memory-mismatch account* (Näätänen, 1992). Corresponding to this interpretation, a vMMN is elicited when the momentary stimulus is incongruent with the sensory memory trace of the repetitive presented standard stimuli. Alternatively to the *sensory-memory-trace variant*, one could argue that a reduction of neuronal activity happens due to adaptation to the standard stimulus and that the deviant (non-adapted) stimulus therefore evokes a stronger neuronal response. However, these accounts cannot be the only explanation for the MMN, since various counter-examples to these theories have been reported. A very striking one has been presented by Kimura and colleagues (2010c). They performed experiments with a traditional randomized oddball sequence. Deviants occurred either randomly or with a fixed oddball sequence, in which exactly every fifth trial was a deviant trial. Although the authors measured a vMMN in both sequences, the strength of the vMMN was significantly reduced in the fixed sequence. This cannot be explained in terms of the *sensory-memory-trace variant* or with neuronal *adaptation*.

Furthermore, a vMMN has been shown for regular sequential patterns (Czigler et al., 2006). Czigler and colleagues presented two different stimuli in a complex pattern. A visual MMN was not elicited by one of the stimuli but by a change in the pattern of stimulus presentation. As a result, the *regularity-representation variant of memory-mismatch account* was suggested. Due to this explanation the vMMN is elicited, because the regular sequential pattern (standard stimulus is followed by a standard stimulus) is violated when a deviant stimulus follows a standard stimulus. Furthermore, this account can explain the reduction in strength of the vMMN for fixed presentation sequences (see above), since in this case a more complex pattern is repeated (e.g. four times stimulus A followed by stimulus B in the sequence A/A/A/A/B/A/A/A/A/B/A/A/A/A/B) and not interrupted. Although the regularity-representation variant of the memory-mismatch account could explain most of the results from vMMN studies, there was still a counter-example reported by Stefanics and colleagues (2011). These authors presented pairs of two different stimuli (for simplicity named A and B). Stimulus pairs of the same stimuli were more frequent (standard: A/A 45%; B/B 45%) than stimulus pairs of two different stimuli (deviant: A/B 5%; B/A 5%). They found a vMMN for the second stimulus in the deviant stimulus pair. Since there was no concrete sequential pattern repeatedly presented this result cannot be explained in terms of the *regularity-representation variant*.

Based on these findings Kimura (2012) proposed a more complex *prediction-error account*. This account states that a vMMN is generated due to violations of an abstract sequential rule in successive visual stimulation. In more detail this implies, that an abstract rule is generated from the preceding stimuli, based on temporal context or temporal structure of the (standard) stimuli. This abstract rule is encoded by a predictive model, which generates predictions for future events. Eventually, these predictions are compared with the current event and a MMN is elicited when this prediction is violated. This process of rule extraction, prediction generation and comparison is assumed to be largely processed automatically. The abstract rule can be a regularity-representation pattern, but can also account for more complex relations.

3 Studies

3.1 Overview of Included Studies

Study I:

SNARC Effect in Different Effectors

Philipp N. Hesse, Katja Fiehler & Frank Bremmer

Perception, 2016, 45(1-2), 180-195.

Study II:

The SNARC Effect in Two Dimensions:
Evidence for a Mental Number Plane

Philipp N. Hesse & Frank Bremmer

In preparation

Study III:

Pre-Attentive Processing of Numerical Visual Information

Philipp N. Hesse, Steffen Klingenhöfer & Frank Bremmer

In preparation

3.2 Aim and Scope of the Studies

For this thesis, I studied processes underlying the human sense of number with psychophysical methods and electroencephalography (EEG) aiming to draw general conclusions on the processing of numerical information. I performed three different studies which are reported in this thesis. The first two studies investigated the effect of *spatial numerical association of response codes* (SNARC). The SNARC effect (Dehaene et al., 1993) is considered evidence that the human brain processes numbers on a *mental number line*, where small numbers are located on the left and large numbers are located on the right. The SNARC effect has been shown for many different response effectors, including bimanual responses, unimanual responses and saccadic responses. My first study investigated the SNARC effect for three different effectors, measured within the same participants, thereby exploring effector dependency of the SNARC effect.

In my second study, I challenged the hitherto set limits of the mental number line (MNL) concept. So far the SNARC effect has been shown for horizontal and vertical orientation but the nature of the underlying number representation was still unclear. For example, it might be that the vertical SNARC effect actually is just a reoriented horizontal SNARC effect (Homes & Lourenco, 2012). In contrast to this, I proposed a *frontoparallel mental number plane* comparable to the transverse mental number plane as recently reported by Chen and colleagues (2015). For this purpose I used a saccadic response setting in order to explore the SNARC effect along the two cardinal axes (horizontal and vertical) as well as the two diagonal axes.

My first two studies, exploring the SNARC effect, focussed on abstract number representations in the so-called *approximate number system* (ANS). Another well documented phenomenon is the human ability to perceive the number of items on very small magnitudes (up to four) immediately. This effect is called *subitizing*. Due to the very fast formation of this percept, subitizing has been seen to be a pre-attentive process, which means that it happens without the need of attentional focus. Anobile and colleagues (2012) showed, however, that subitizing was influenced by attentional load and concluded that it actually would not be pre-attentive. In my third study, I applied EEG measurements to utilise the effect of *visual mismatch negativity* (vMMN) to provide evidence for the pre-attentive processing of small stimulus amounts in the subitizing range.

3.3 Common Concept of Study I and Study II

3.3.1 Introduction

For many issues of our everyday life, numbers and number perception are fundamental. Accordingly, from a neuroscientific perspective, it is important to understand where and how the human brain processes numbers. There are several indications that number representations in the human brain "interact" with spatial representation in a characteristic way. For instance, digits induce a bias to the left for small numbers and to the right for large numbers, when subjects are instructed to freely choose whether to press a left or a right button as a response to their visual presentation (Daar & Pratt, 2008). The strong link between numbers and space in the human brain can also be deduced from findings showing that saccadic eye movements influence number or magnitude perception (e.g. Irwin & Thomas 2007; Burr et al. 2010a; Binda et al. 2011, 2012).

Another example concerns the finding that in a magnitude comparison task in which subjects had to decide whether digits were smaller or larger than a reference number (e.g. 5) they reacted faster to the left for small numbers and faster to the right for large numbers (Dehaene et al., 1990). Remarkably, the number magnitude did not necessarily need to be processed explicitly to induce this effect. Instead, with the discovery of the SNARC effect (spatial numerical association of response codes) Dehaene and colleagues (1993) showed that human subjects react faster to the left for small numbers and to the right for large numbers, when judging number-parity indicated with button-presses using the left and right hand. In general, the SNARC effect is seen as an indication of the concept of the *mental number line* (MNL) which states that humans organize numbers on a mental line with small numbers on the left and large numbers on the right.

Since its discovery, numerous follow-up studies on the SNARC effect have aimed to determine experimental parameters and cognitive settings causing or modulating it.

Reading- and writing-directions have been identified as such a parameter. Subjects who write from right to left revealed an inverted SNARC effect (Dehaene et al., 1993). The SNARC effect has been reported for different other stimulus sets than Arabic digits, such as written number words, dice patterns, spoken number words (Nuerk et al., 2005) or Chinese digits (Kopiske et al., 2015; but see Hung et al., 2008). The SNARC effect can not only be observed for response latency, but also for response accuracy: answers for large numbers were more likely to be wrong, if requested response direction was left instead of right and vice versa (Schwarz & Keus, 2004; Keus & Schwarz, 2005; Nuerk et al., 2005; but see Wood et al., 2006a).

Furthermore, the SNARC effect has been shown for different effectors such as bi-manual responses (Dehaene et al., 1993), unimanual pointing responses (Fischer, 2003; Bingel & Heath, 2011), saccadic eye movements (Schwarz & Keus, 2004) and pedal responses (Schwarz & Müller, 2006). Other findings showed that the SNARC effect is likely linked to response representations (Gevers et al., 2006b) rather than (early) stimulus representations. In my first study with the title *SNARC Effect in Different Effectors* (see chapter 3.4) I tested the hypothesis of an effector independent SNARC effect by comparing the strength of the SNARC effect measured in a group of subjects for three different effectors (finger release, arm pointing and saccadic eye movements). If the SNARC effect was effector independent, one would expect a strong pairwise correlation between two effectors. Alternatively a lack of correlations would point to an effector dependent SNARC effect.

My second study aimed to investigate a different property of the SNARC effect. So far the SNARC effect has been shown for both cardinal axes in a frontoparallel plane with bi- and unimanual button presses (Ito & Hatta, 2004; Gevers et al., 2006b; Holmes & Lourenco, 2011, 2012; Shaki & Fischer, 2012; Hartmann et al., 2014) and saccadic eye movements (Schwarz & Keus, 2004). Ito & Hatta (2004) assumed a vertical orientation with small numbers at the top and large numbers at the bottom, due to writing habits of their Japanese subjects. In contrast to this assumption they found a SNARC effect along the vertical axis with shorter latencies for small numbers at the bottom and large numbers at the top. These results were further confirmed by Gevers and colleagues (2006b), Shaki and Fischer (2012), Schwarz and Keus (2004) and Hartmann and colleagues (2014) in western subjects (but see Hung et al., 2008 for Chinese subjects). Several hypotheses concerning the cognitive basis of this finding were proposed, among them the levels of a skyscraper (rising from bottom to top), or measuring the height of objects.

One important aspect concerning a SNARC effect along the vertical axis concerns the response mode: in some of these studies (Ito & Hatta, 2004; Gevers et al., 2006b; Holmes & Lourenco, 2011 (Exp. 1); Shaki & Fischer, 2012) responses for the “vertical” axis were measured with button presses on a computer keyboard which was ordinarily placed on a table. Hence, the responses were given in the transverse plane (on the mid-sagittal axis) and would better be described as “near” and “far” than as “down” and “up” (see Holmes & Lourenco, 2011, 2012; Hartmann et al., 2014; Winter et al. 2015, for the same issue). The sagittal axis has been investigated by other studies, too. Here, in congruency with the above mentioned reported results, small numbers were associated with “near” and large numbers were associated with “far” (e.g. Chen et al., 2015). Interestingly, the SNARC effect in depth was found to be *isotropic*, i.e. it occurred only in terms of “far” vs. “near” but not in terms of “in front” vs. “behind”.

Other studies which investigated a vertical SNARC effect by means of responses along the vertical axis found differences in strength of the SNARC effect on this axis. For saccadic eye movements a strong vertical SNARC effect was found (Schwarz & Keus, 2004). For button presses along the vertical axis a significant SNARC effect was reported by Hartmann and colleagues (2014, Exp. 1). Interestingly no vertical SNARC effect was found when responses were given with one hand on top and one foot at the bottom (Hartman et al., 2014, Exp. 2-4). In contrast to these findings, Holmes and Lourenco (2011, 2012) reported a significant vertical SNARC effect solely when subjects were “primed” with vertical numerical magnitude (e.g. levels in a building) and no significant vertical SNARC effect for “unprimed” (naïve) subjects.

Gevers and colleagues (2006b) and Holmes and Lourenco (2011, 2012) investigated the SNARC effect also along a diagonal axes. Although experiments differed in methods (as mentioned above, Gevers and colleagues (2006b) recorded button presses in the transversal plane), both studies received more or less the same results. They found a strong SNARC effect on one diagonal axis (named “right-diagonal” or “congruent diagonal”) that required responses to up-right and down-left. On the other diagonal axis (“left-diagonal” or “incongruent diagonal”) that required responses to up-left and down-right, no SNARC effect was found. The observation that no SNARC effect was found on the “left-diagonal” has been explained by Gevers and colleagues by the fact that along this diagonal two incongruent “categories” were activated: For example, number “1” should be responded faster to the left and to the bottom. When investigating the “left-diagonal” participants’ answers to “left up” could be faster due to congruence with “1” and “left”, but participants’ answers could also be faster to “right down” due to congruence with “1” and “down”, hence resulting in no advantage for any response-direction. In contrast, Holmes and Lourenco interpreted their results as evidence that there would be no (or only rare) *spontaneous vertical organization of numbers*. They assumed that any vertical SNARC effects would therefore be a result of a “trump”, a kind of “overrulement”, of the horizontal SNARC effect.

The above mentioned studies do have in common that subjects were only tested for a SNARC along the diagonal axes. Accordingly, it was impossible, to infer subjects’ performance along the diagonal axis from their performance along the horizontal and vertical axes. Consequently, in my second study titled *The SNARC Effect in Two Dimensions: Evidence for a Mental Number Plane* (see chapter 3.5), I measured SNARC effect along four axes (horizontal, vertical and both diagonals) <u>within the same participants</u>, which allowed me to predict diagonal behaviour from behaviour for the cardinal axes and to compare predictions with measured data. My data clearly show that the SNARC effect on the diagonal axes can be described as a linear combination of the participants’ SNARC behaviour along the cardinal axes. My results provide further evidence for the idea of a frontoparallel SNARC plane and, ultimately, the idea of a *frontoparallel mental number plane*.

3.3.2 Common Methods

3.3.2.1 Participants

A total of 32 participants (nine male) aged between 20 and 28 (mean 23.3) for study I and 28 participants (eleven male) aged between 20 and 31 (mean 25) for study II were recruited from the university population. Some subjects participated in both studies. All participants had normal or corrected to normal vision and were native German speakers. In study I all participants were right handed and performed three SNARC-like tasks, adapted for three effectors. In the second study participants performed two saccadic SNARC-like tasks, adapted for two sensory modalities (*auditory* and *visual*). All subjects except one (the author only participating in study II) were naïve to the purpose of the study and were compensated with 6 € or 8 € per hour (compensation was increased over data collection time for external reasons) for participation. After completing the full experiment each interested participant was given full disclosure concerning the purpose of the experiment. Participants provided written informed consent before commencing the experiment and all procedures were approved by the local ethics committee and were in agreement with the Declaration of Helsinki.

3.3.2.2 Setup

Experiments were performed in a dark and sound attenuated room. Participants sat on a chair resting their head on a chin rest placed centrally in front of a screen. The distance between the screen and the participants' eyes was 45 cm in study I and 70 cm in study II. In my first study the screen was a 39 cm (46.9°) wide and 29.5 cm (36.3°) high CRT display (Iiyama Vision Master Pro 513). Resolution was set to 1152 x 864 pixels and the refresh rate was set to 100 Hz. In the second study the screen was 120 cm (81°) wide and 90 cm (65.5°) high. All visual stimuli were back-projected on this screen by a video-projector (Christies DS+6K-M, Christie Digital Systems Canada Inc., Kitchener, Canada). The resolution of the screen was set to 1152 x 864 pixels and the refresh rate to 60 Hz. In both studies participants' eye positions were recorded with an EyeLink II (SR Research Ltd., Ottawa, Canada) at a sampling rate of 500 Hz.

3.4 Study I: The SNARC Effect in Different Effectors

3.4.1 Methods

3.4.1.1 Setup

In addition to the common settings described above three buttons were attached to the screen and three buttons were placed in front of the screen (see Figure 3-1). The central button placed before the screen was aligned to the middle of the screen (labelled "Finger / Eye ready" in Figure 3-1). Two buttons (labelled "Finger response") were fixated with a distance of 14 cm to the left and to the right. All three buttons had a size of 1 cm x 1 cm

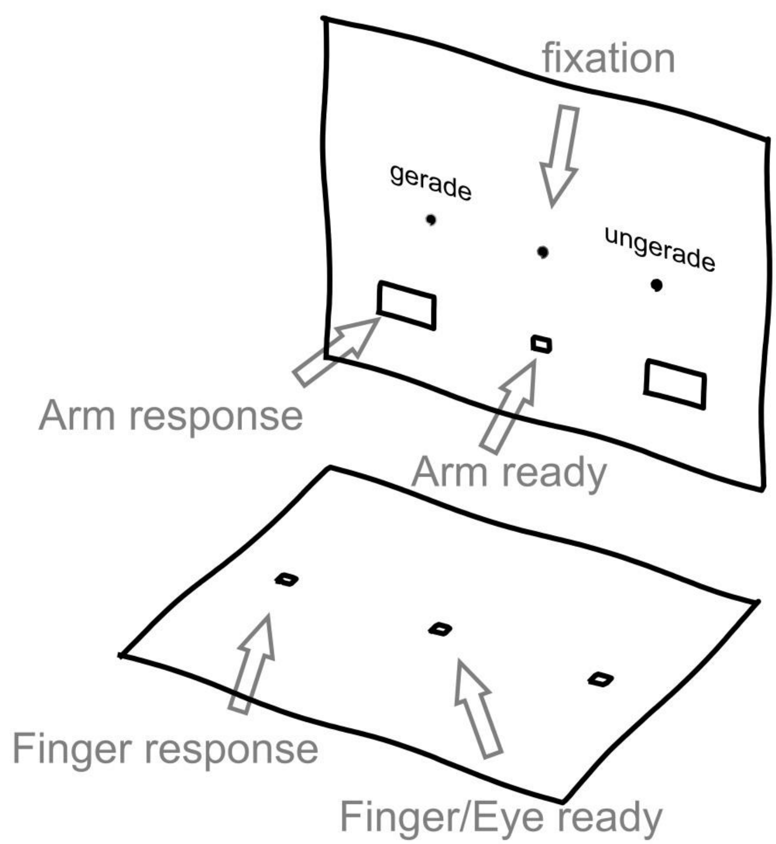


Figure 3-1: Sketch of the used setup. All buttons were attached permanently. The words odd and even (in German "gerade" and "ungerade") were drawn in white (luminance: 25 cd/m²) on a grey background (1 cd/m²) and switched location depending on the task. (Hesse et al., 2016)

and were placed 15.5 cm in front of the screen. The other three buttons, which were attached to the screen, were placed 8 cm below the midline of the screen. The central button (labelled “Arm ready”) had a size of 1 cm x 1 cm, too. The two remaining buttons (labelled “Arm response”) were placed 14.9° to the left and to the right and had a larger size of 5 cm x 2.5 cm (5.9° x 3.1°). All changes on the six buttons (presses and releases) were recorded by the EyeLink II with a sampling rate of 500 Hz.

3.4.1.2 Stimuli

During the experiment a white fixation point (luminance: 25 cd/m²) in the middle of the screen and white headlines (luminace: 25 cd/m²) with the German words for odd and even (“ungerade” and “gerade”) were presented all the time on a grey background (luminance: 1 cd/m²). Headlines were presented 3° above and 10° to the left and to the right of the fixation point. In one of the three tasks, when subjects had to respond with saccades (see chapter 3.4.1.3 Procedure), two grey points (saccade targets) were presented 10° left and 10° right of the fixation point on the vertical midline of the screen.

Stimuli were spoken words, presented via headphones (mean sound pressure level 75.8 dBA) for all effectors. Sound files were generated by a commercially available text-to-speech algorithm (MWS Reader Version 3, http://www.mwsreader.com). Stimuli consisted of the German number words “eins”, “zwei”, “drei”, “vier”, “sechs”, “sieben”, “acht” and “neun” which are the numbers one to nine except five. Furthermore, 18 German nonnumber words were selected from the Leipzig Corpora Collection (Quasthoff et al., 2006; the 2010 German corpus) for each number word. Those nonnumber words were chosen to match the number words in *frequency class* (see chapter 6.1 Appendix A1). This resulted in 144 additional nonnumber words which were used in catch trials. With the catch trials a behavioural response of the participants before properly recognising the stimulus, should be avoided. For practice trials twelve extra nonnumber words were chosen.

3.4.1.3 Procedure

Participants were instructed to judge the parity of the presented number in non-catch trials as precisely and as quickly as possible. Responses were made on/to the left or on/to the right side depending on the applied response mapping and the parity of the presented number. Responses were given with one of three different effectors. These effectors were: fingers of both hands (this condition and data of this condition is hereafter referred to as *Finger*), saccadic eye movements (*Eye*) and unimanual pointing movements (*Arm*). In catch trials which were trials with nonnumber words presented participants were instructed to withhold their reaction. Subjects had to fixate the central fixation point (except in condition *Eye*, see below) through the whole trial. Trials were aborted and repeated when gaze position erroneously left an invisible, electronically defined window of 2.6° x 2.6° around the fixation point. Each trial was started by a drift-correction that was conducted by pressing the "Finger / Eye ready" button or the "Arm ready" button. Drift-correction ensured the stability of eye-tracking measurement over time.

In condition Finger subjects had 750 ms after drift correction to press the "Finger response" buttons. The left button had to be pressed with the index finger of the left hand and the right button with the index finger of the right hand. Buttons had to be released according to the correct response side depending on the parity of the number and applied response mapping. In catch trials both buttons had to be pressed for another 2 s after stimulus onset. In this condition the time between stimulus onset and button release was defined as reaction time (RT).

In condition Eye subjects had to maintain fixation until stimulus onset. Then a saccade to one of the two in this condition peripherally displayed points (saccade targets) had to be made according to stimulus parity and used response mapping. Trials ended when the saccade was performed. In catch trials no saccade had to be performed and the trial ended 2 s after stimulus onset. Saccades were defined as eye movements that reached or exceeded 80°/s. The onset of the saccade was chosen as the point in time and space where eye velocity first reached 20°/s. Saccade offset was taken as the time and space where eye velocity fell below 20°/s. RT was defined as time between stimulus onset and saccade onset.

In condition Arm subjects had to press the “Arm ready” button within 750 ms after drift-correction with the index finger of their right hand. After stimulus onset participants had to release the “Arm ready” button and press one of the “Arm response” buttons with their right index finger. Again the correct side depended on stimulus parity and applied response mapping. In catch trials participants had to keep the “Arm ready” button pressed for additional 2 s. Reaction time in the condition was defined as time between stimulus onset and the release of the “Arm ready” button.

The three different effectors were tested on three different not necessarily subsequent days (sessions). At each session one effector was tested in two sets, starting with one response mapping, for example left odd and right even, followed by the remaining response mapping (left even, right odd) in the second set. Between both sets participants had a break of at least 20 minutes to reduce the probability of confusion between response mappings. The order of mappings was counterbalanced between subjects. Effector Finger and effector Eye were measured counterbalanced, while effector Arm was always measured as last effector. This resulted in an average time between measurements of Finger and Eye of 9 days, while time between measurement of the second effector and effector Arm was 44 days on average.

Within one set every number was presented 27 times (8 x 27 = 216 number trials) together with 24 distractor words, resulting in a total amount of 240 trials in each set. At the beginning of each set participants performed ten practice trials to become familiarized with the response mapping and the task. The ten practice trials consisted of the eight numbers and two distractor words.

3.4.1.4 Analyses

Before starting the main analysis all trials with incorrect responses as well as outliers and catch trials were removed. All trials were considered as outliers that had RTs outside the range of mean ± 3 standard deviations. Furthermore, the trials in the saccadic task were removed as well in which saccades started outside a ± 3.8° window around the fixation point or ended closer than 8.8° to the fixation point. Due to this procedure 183 trials in the saccadic task were removed.

At first, I verified the presence of a SNARC effect in each effector. This was done by the method introduced by Dehaene and colleagues (1993). For each subject and effector I calculated the difference between median RTs (median RT to the right minus median RT to the left). Then I regressed these differences with a linear function of number. Finally a one-sided t-test was performed to test whether slopes of the linear regressions were significantly below zero. Another method to determine the existence of a SNARC effect was to separate the reactions in SNARC compatible (i.e. 1 to 4 to the left and 6 to 9 to the right) and SNARC incompatible (c.f. Jarick et al., 2009). The median RT was taken within each participant and effector. Than for each effector a one-sided t-test was applied to test, whether the difference (SNARC compatible minus SNARC incompatible) was below zero. As a third method I used a repeated measures *analysis of variance* (ANOVA) conducted on median RTs (c.f. Nuerk et al., 2005). As factors *magnitude* (1 & 2, 3 & 4, 6 & 7, 8 & 9), *response side* (left, right) and *parity* (even, odd) were used. In such an ANOVA a SNARC effect is represented by a significant interaction between *magnitude* and *response side* together with a mean negative slope of the linear regressions (p values were adjusted for multiple testing to an alpha level of .05 using a false discovery rate (FDR) correction; Benjamini & Hochberg, 1995).

The aim of my study was to compare the SNARC strength between effectors. The analyses explained above provided two potential indicators for SNARC strength, the slope of the linear regression in the first analysis and the RT difference between compatible and incompatible trials in the second analysis. Both parameters become more negative with increasing SNARC strength. To reduce the amount of analyses, I investigated the Pearson product-moment correlation between both SNARC strength parameters. Due to their high correlation (see chapter 3.4.2 Results) I confined my further analyses to the slope of the linear regression, as this is the generally more common parameter for SNARC strength. In a next step I calculated the Pearson product-moment correlation pairwise between the

SNARC strength of two effectors. The assumption of an effector independent SNARC effect predicted a high correlation between the strengths of the SNARC effect in the different effectors. On the contrary a lack of significant correlations would indicate an effector dependent SNARC effect.

Due to the results of this first analysis, I applied a second analysis on my group data. Therefore, I counted for each effector pair (called X and Y for simplicity hereafter) how many subjects showed a SNARC effect in both effectors (X and Y), only in one effector (X but not Y, or Y but not X), or in no effector (neither X nor Y). With a Fisher exact test I determined whether the amount of subjects demonstrating a SNARC effect in both effectors differed significantly from the amount expected if SNARC effect were effector unspecific or effector specific. Findings in literature showed that on average two thirds of participants in a group showed a SNARC effect (Nuerk et al., 2004; Wood et al., 2006a; Viarouge et al., 2014b). In combination with Bayes rules on conditional probabilities this allows conclusions on the expected probability to find a SNARC effect pairwise in two effectors. Mathematically, the probability $p(X \cap Y)$ to find a SNARC effect in effector X <u>and</u> in effector Y is given by

$$p(X \cap Y) = p(X|Y) \cdot p(Y). \quad (2)$$

In this equation $p(X \mid Y)$ is the probability of SNARC in effector X given its occurrence in effector Y. p(Y) is the probability of SNARC in effector Y. This equation can be transformed to

$$p(X|Y) = p(X \cap Y) \ / \ p(Y). \quad (3)$$

If the SNARC effect was effector *specific* p(X), the probability of finding SNARC in effector X, would by definition be statistically independent of p(Y), the probability of finding SNARC in effector Y, which leads to this equation:

$$p_{Spec}(X \cap Y) = p(X) \cdot p(Y). \quad (4)$$

If, on the other hand, the SNARC was effector *unspecific* the occurrence of SNARC in one effector would predict its occurrence in the other effector. This leads to the probability of finding SNARC in effector X given a SNARC effect in effector Y:

$$p_{Unspec}(X|Y) = 1. \tag{5}$$

Hence, the probability to find SNARC in both effectors given the SNARC was effector unspecific is:

$$p_{Unspec}(X \cap Y) = p_{Unspec}(X|Y) \cdot p(Y) = p(Y). \tag{6}$$

These calculations can be extended towards observations of three effectors. Given SNARC was effector specific the probabilities p(X), p(Y), and p(Z) of the occurrence of SNARC in the effectors X, Y, and Z were statistically independent. This would lead to the following probability:

$$p_{Spec}(X \cap Y \cap Z) = p(X) \cdot p(Y) \cdot p(Z). \tag{7}$$

If, on the other hand, SNARC was effector unspecific, then the probabilities p(X), p(Y), and p(Z) of the occurrence of SNARC in the effectors X, Y, and Z were statistically dependent. In other words, in such case, the occurrence of SNARC in effector X would be predictive of occurrence of SNARC in effectors Y and Z which would lead to the following probability:

$$\begin{aligned} p_{Unspec}(X \cap Y \cap Z) &= p(X) \cdot p_{Unspec}(X \cap Y) \;/\; p(X) \cdot p_{Unspec}(X \cap Y \cap Z) \;/\; p_{Unspec}(X \cap Y) \\ &= p(X) \cdot p_{Unspec}(Y|X) \cdot p_{Unspec}(Z|(X \cap Y)) \\ &= p(X) \cdot 1 \cdot 1 \\ &= p(X) \end{aligned} \tag{8}$$

3.4.2 Results

In total, 46,080 trials were performed by 32 subjects. Due to outlier removal 174 trials (1.3%) in condition Finger, 197 trials (1.4%) in condition Eye and 143 trials (1.0%) in condition Arm were removed from further analysis along with 390 trials (2.8%) in condition Finger, 768 trials (5.5%) in condition Eye and 144 trials (1.0%) in condition Arm in which wrong answers were given. Finally 13,260 trials (95.9%) in condition Finger, 12,676 trials

(91.7%) in condition Eye and 13,537 (97.9%) in condition Arm remained. Mean reaction times (RT) were 664 ms (Finger), 573 ms (Eye) and 576 ms (Arm).

3.4.2.1 The SNARC Effect in Different Effectors

Overall mean RTs were for Finger: right: 654 ms; left: 646 ms, for Eye: right: 556 ms; left: 558 ms, and for Arm: right 562 ms; left 577 ms. A detailed list of mean RTs is listed in Appendix A2 (see chapter 6.2). Analysis of regression slopes over median RT differences revealed a clear SNARC effect for Finger (slope: –2.83 ms/number; see Figure 3-2 A) and Eye (slope: –3.11 ms/number; see Figure 3-2 B) but solely a small SNARC effect in effector Arm (slope: –0.15 ms/number; see Figure 3-2 C). The one-sided t-test at the group level showed significant negative slopes for effector Finger, t(0.95; 31) = –2.18, p = .022, and effector Eye, t(0.95; 31) = –2.58, p = .017, but not for Arm, t(0.95; 31) = –0.24, p = n.s. (all p values FDR corrected).

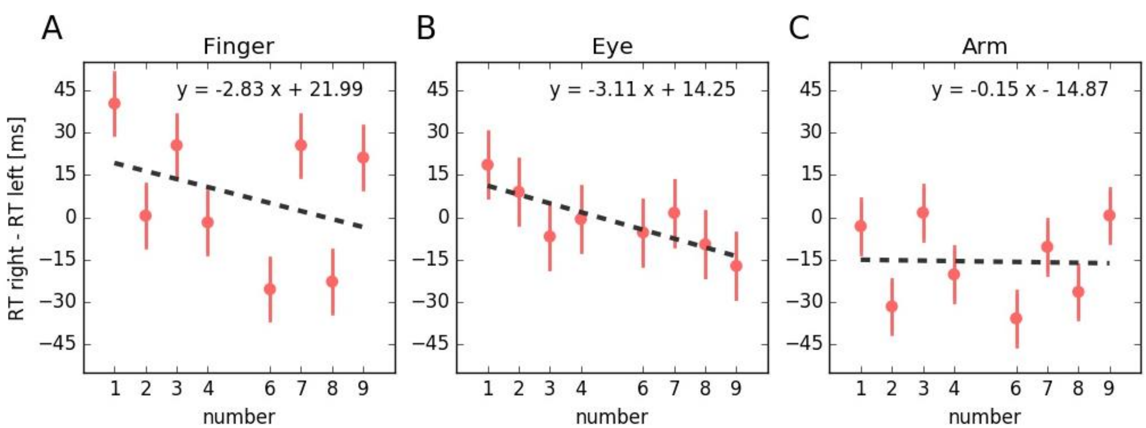


Figure 3-2: Differences in median reaction time responses on the right side and on the left side for each number (red dots) averaged across participants. Error bars indicate standard error of the mean. In such a plot a SNARC effect is indicated by a greater difference for low numbers and a smaller difference for high numbers. This results in a negative slope of the linear regression (dashed line). (Modified from Hesse et al., 2016)

The analysis of compatible and incompatible reaction times showed a negative difference (compatible minus incompatible) for all three effectors. Median RT-differences were: –6.65 ms (Finger), –6.42 ms (Eye) and –3.05 ms (Arm). The one-sided t-test over participants within each effector revealed that these differences were significantly negative (Finger: $t(0.95; 31) = -1.89$, $p = .034$; Eye: $t(0.95; 31) = -2.14$, $p = .030$; Arm: $t(0.95; 31) = -2.20$, $p = .030$; all p values FDR corrected). In contrast to the slope analysis this results clearly demonstrated a SNARC effect in each effector.

As a third analysis a three-way repeated measures ANOVA was conducted with *magnitude*, *parity* and *response side* as parameters (see chapter 3.4.1.4 Analyses). The ANOVA was applied on median RT separately for each effector. As described above a significant interaction of *magnitude* and *response side* along with a negative mean slope in the slope analysis would indicate a significant SNARC effect. For all three effectors the interaction *magnitude* x *response side* was significant: Finger: $F(3,93) = 4.13$, $p = .017$; Eye: $F(3,93) = 5.07$, $p = .016$; Arm: $F(3,93) = 3.55$, $p = .022$ (all p values FDR corrected). Together with the above described negative mean slopes in every effector these results proved the existence of a significant SNARC effect in each effector. Along with the test for a significant SNARC effect another number related effect, the MARC effect (linguistic markedness of response codes; Berch et al., 1999; Nuerk et al., 2004; see chapter 2.1.2.2 The MARC Effect), could be investigated with the ANOVA. The MARC effect can be proved by a significant interaction between *parity* and *response side* in this kind of ANOVA. Such a significant interaction was found for effector Finger ($F(1,31) = 14.86$, $p < .001$) and effector Arm ($F(1,31) = 6.48$, $p = .016$) but not for effector Eye ($F(1,31) = 0.002$, p = n.s.).

As described in the methods (see chapter 3.4.1.4 Analyses) the SNARC strength can either be estimated as the slope of the linear regression or as the difference in median RTs between compatible and incompatible trials. I conducted a Pearson product-moment correlation between both SNARC strength estimates (see Figure 3-3). The correlation between both parameters was highly significant (all $p < .001$). Hence, I could decide to choose one of the two parameters for further analysis. Since the slope method is more common in SNARC literature I decided to proceed with the slope of the linear regression over reaction time differences between answers to the left and to the right as parameter for the strength of the SNARC effect.

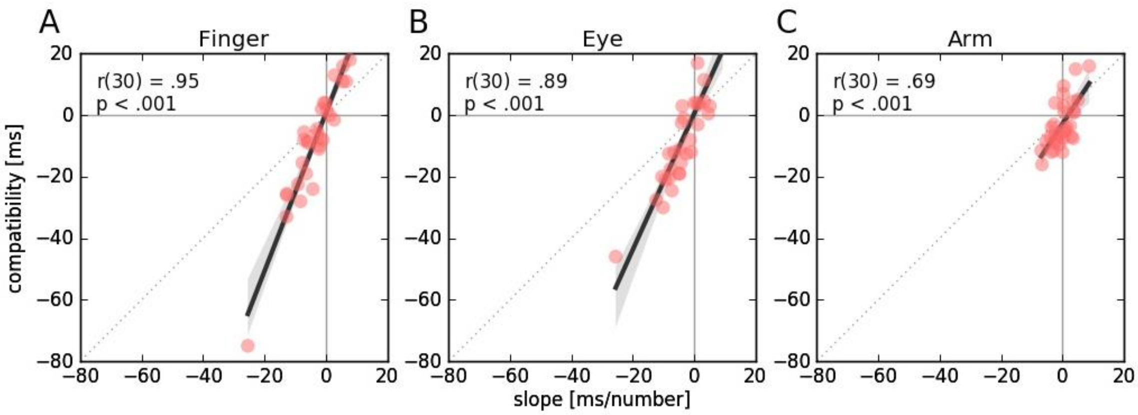


Figure 3-3: Comparison of the slope-estimate and the compatibility-estimate. Each data point in each panel shows for a given participant the SNARC strength as determined by slope-method (abscissa) and the compatibility-method (ordinate). Grey shaded areas indicate 95% confidence interval of regression slope (black line). Data are shown for effector Finger (A), Eye (B) and Arm (C). For each effector the two different measures of SNARC strength were highly correlated (all r(30) > .69, all p < .001) and hence, confirmed that the two estimates had high criterion validity.

3.4.2.2 Effector-Specific Spatial Mapping of Numbers

The main purpose of this study was to determine whether the SNARC effect is effector dependent or not. If the SNARC effect was effector independent, one would expect significant correlations between the slopes of the linear regression of different effectors as SNARC strength estimates. On the contrary a lack of significant correlations would indicate an effector-dependency of the SNARC effect. The pairwise comparison of the three effectors (see Figure 3-4) revealed a significant Pearson product-moment correlation between effectors Finger and Arm ($r(30) = .52$, $p = .002$). No significant correlation was found between effectors Eye and Finger ($r(30) = .19$, $p = .30$) and between Eye and Arm ($r(30) = .26$, $p = .15$).

Since the SNARC effect might be effector-independent even without a significant correlation between the SNARC strength estimates I performed an additional analysis based on the probability to find participants that show a SNARC effect in both effectors. In order to do so, I determined for each effector pair the amount of participants showing a SNARC effect in both effectors (termed X and Y hereafter), or only in one effector (X but

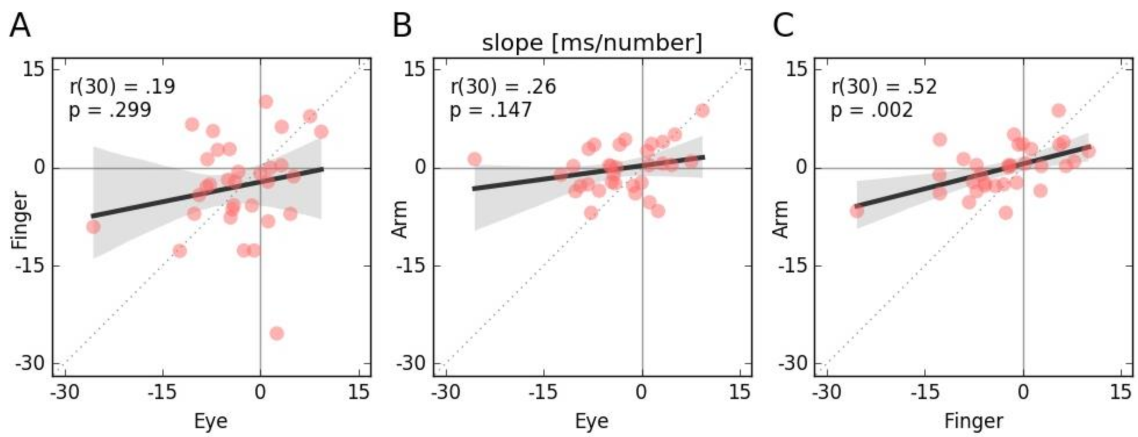


Figure 3-4: Comparison of SNARC strength in the three effector pairs. Eye-Finger (A), Eye-Arm (B) and Finger-Arm (C). Each data point (red circles) represents data from a single subject. Grey shaded areas indicate 95% confidence interval of regression slope (black line). Pearson Rho results for correlations are written inside the figure. I found a significant correlation between Finger and Arm, but not for Eye and Finger or Eye and Arm. (Modified from Hesse et al., 2016)

not Y or Y but not X), or in no effector at all (neither X nor Y). This grouping is equal to the amount of data points in Figure 3-4 in the upper right quadrant (I. no SNARC in any effector), the upper left quadrant (II. SNARC in X but not in Y), the lower left quadrant (III. SNARC in both effectors), and the lower right quadrant (IV. SNARC in Y but not in X). The determined amounts are presented in Table 3-1.

Table 3-1: Number of data points in Figure 3-4 in the four quadrants, representing a negative slope in no effector (quadrant I), in effector X (quadrant II), in both effectors (quadrant III) and in effector Y (quadrant IV) for all three combinations of effectors. The proportions are given below.

A

Finger \ Eye	–	+
+	5 15.5%	5 15.5%
–	16 50%	6 19%

B

Arm \ Eye	–	+
+	9 28%	9 28%
–	12 38%	2 6%

C

Arm \ Finger	–	+
+	9 28%	9 28%
–	13 41%	1 3%

In my data a SNARC effect was present on average in about two thirds of the participants (Finger: n = 22; Eye: n = 21; Arm: n = 14). This was pretty well in line with values found in literature (Nuerk et al., 2004; Wood et al., 2006a; Viarouge et al., 2014b). Resulting from equation (4) (see chapter 3.4.1.4 Analyses), I expected a SNARC effect in both effectors in 44% of my participants if the SNARC effect was effector-dependent, which means specific for the effector. Hence, from 32 participants 14 subjects showing a SNARC effect in both effectors would have been expected in this case. Accordingly, 21 subjects showing a SNARC effect in both effectors would have been expected if the SNARC effect was effector-independent, which means effector unspecific (compare equation (6)). The amount of subjects showing SNARC in both effectors (see Table 3-1) differed significantly from what one would have expected if SNARC effect was effector unspecific (tested with a Fischer exact test) for effector pairs Eye-Arm ($p < .02$) and Finger-Arm ($p < .03$). For effector pair Eye-Finger the test revealed a close to significant trend ($p = .09$). On the contrary the reported amount did not differ significantly from what one would have expected if SNARC effect was effect specific (all $p > .17$).

Similar results were obtained, when comparing all three effectors together. According to equation (7) and equation (8) one would expect ten subjects showing SNARC in all three effectors, if SNARC effect was effector-dependent and 21 subjects, if SNARC effect was effector independent. In my dataset eleven participants showed a SNARC effect in all three effectors. Again the proposed amount for an effector-independent SNARC effect differed significantly from the amount I found in my subjects ($p < .01$) but not from the assumption for an effector independent SNARC effect ($p > .2$).

3.4.3 Discussion

The central aim of my study was to determine whether the SNARC effect is effector unspecific, or effector specific. 32 participants performed an auditory parity judgment task with three different effectors: Finger, Eye and Arm. As a first step of my analysis I proved that a SNARC effect was present in each effector individually. A SNARC effect, i.e. a negative linear regression slope, was on average present in two out of three subjects for effectors Finger and Eye, which is in line with other studies (Nuerk, et al., 2004; Wood et al., 2006a; Viarouge et al., 2014b). About half of the subjects showed a SNARC effect in effector Arm.

I propose that my results indicate a distributed neural basis of the SNARC effect. If the SNARC strength found in one effector was correlated with the SNARC strength found in the other two effectors, this would have pointed to a common sensory-to-motor mapping of the investigated effectors. Given the different motor-control networks controlling the three measured effectors such a result would have required the existence of a single SNARC effect module (or brain site). Given findings that the SNARC effect is related to response representations rather than stimulus representations (Keus et al., 2005; Gevers et al., 2006b), this intermediate brain site could be a network in the parietal cortex, where neurons are assumed to be late in sensory processing but early in motor processing (Andersen, 1995; Shulman et al., 2002). Furthermore, this would have fit with discoveries from Nicholls and colleagues (2013) that attentional shifts were in accordance with the mental number line, even when responses were not mapped correspondingly. In addition, Cutini and colleagues (2012) showed that parietal areas were active during a SNARC task, which would support the theory of an effector-unspecific SNARC effect source.

However, from three investigated correlations of SNARC strength between different effectors, only one correlation was significant. Hence, I propose that the sensory-to-motor mapping underlying the SNARC effect is isolated for each effector, or at least not as close as thought before. Thus, my results imply a distributed SNARC-brain-network.

The one correlation I found was for the strength of the SNARC effect between effector Finger and effector Arm. This was, at first sight, different from the finding of “no correlation” between the other two effectors pairs and maybe could be explained by the experimental paradigm I used. When effector Arm was measured, subjects used their right index finger, as a part of their arm, to respond to the presented stimulus. Hence, it might be, that the sensory-to-motor mapping for effector Arm overlapped with the sensory-to-motor mapping employed in sessions in which effector Finger was measured. This (partial) overlap might have led to no strict separation of the two effectors and could explain the correlation in SNARC strength between effector Finger and effector Arm. However, the majority of the correlations (Eye-Finger and Eye-Arm) did not reveal a relationship between the underlying sensory-to-motor mappings governing the SNARC effect strength.

This more or less disputable result led me to perform a second analysis based on relative SNARC occurrence in the three different effectors. The ratio of this approach was that if the SNARC effect was effector unspecific, the likelihood to find SNARC in one effector should forecast the occurrence in another effector. It is known from literature (e.g. Nuerk et al., 2004; Wood et al., 2006a; Viarouge et al., 2014b) that the SNARC effect occurs in roughly two out of three subjects. This was also the case in my study (60%). I compared the amount of participants showing a SNARC effect on both effectors with the expected amount if SNARC effect was effector unspecific (which is statistically dependent) or effector specific (which is statistically independent) based on the literature value (66%). In all cases the amount of participants did not differ significantly from what one would expect if the SNARC effect was effector specific. In contrast in three fourth of all comparisons the observed amount differed significantly from the expected amount if SNARC effect were effector unspecific. Thus, my results in this second analysis point towards an effector-specific SNARC effect.

One could argue that the fixed experimental schedule together with the fact that effector Arm was always the last measured effector, might have influenced my results, since the test-retest reliability of the SNARC effect might be weaker as assumed so far (e.g. Viarouge et al., 2014b). On the contrary a significant correlation between the quantity of grey matter in a subregion of the human posterior parietal cortex and the strength of the SNARC effect in these participants has been found (Krause et al., 2014). These results strongly imply a reliability of the SNARC effect within participants over time.

3.5 Study II: The SNARC Effect in Two Dimensions: Evidence for a Mental Number Plane

3.5.1 Methods

3.5.1.1 Stimuli

A white fixation point (luminance: 134 cd/m^2) in the middle of a grey screen (luminance: 30 cd/m^2) was shown throughout all trials. Saccade targets were shown on opposite sides of the fixation target, either on the horizontal or vertical meridian or on a diagonal. From here on I will use the terms "Horizontal", "Vertical", "Diagonal_1:30" and "Diagonal_4:30" as reference to these four axes (see Figure 3-5). Thereby Diagonal_1:30 (half past one on a clock) describes the diagonal going from "right up" to "left down" and Diagonal_4:30 (half

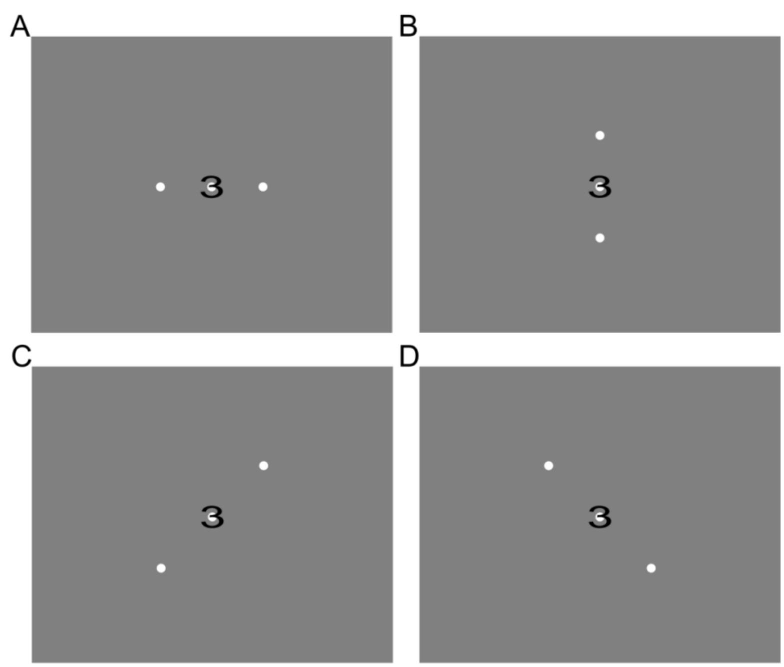


Figure 3-5: Illustration of the displayed stimuli (not drawn to scale). The screen had a grey background (30 cd/m²), dots (fixation point as well as saccade targets) were drawn in white (134 cd/m²) and numbers (if presented visually) in black (0.2 cd/m²). Saccade targets were drawn on Horizontal (A), Vertical (B), Diagonal_1:30 (C) or Diagonal_4:30 (D) axis with 11.5° (A and B) or 16.3° (C and D) distance to the fixation point.

past four) the other diagonal. The distance from the fixation target to the saccade targets was either 11.5° (for targets on the meridians) or 16.3° (for targets on the diagonals). Fixation point and saccade targets had the same size (radius = 0.2°). Subjects had to judge the parity of numbers between 1 and 9, except 5. In the visual task, numbers were black digits (luminance: 0.2 cd/m², size: 3° x 3°) centred on the fixation point and were presented for 33 ms. In the auditory task, stimuli were the German words for the numbers (in German: “eins”, “zwei”, “drei”, “vier”, “sechs”, “sieben”, “acht” and “neun”) presented via headphones (mean sound pressure level 73.6 dBA). Auditory stimuli had been recorded beforehand by a female human speaker and were clearly understandable.

3.5.1.2 Procedure

On each trial the participants made a judgment on the parity of the presented number. Responses were made with saccadic eye-movements from the central fixation point to one of the two peripheral saccade targets. “*Response mappings”* required reporting odd numbers by means of a saccade to the one point and even numbers to the other or *vice versa*. Saccade targets positions were on the horizontal meridian, the vertical meridian or on one of the two diagonals (see Figure 3-5) and I will refer to these response orientations hereafter as “*axes*”. Participants were instructed to respond both quickly and accurately. In total, 16 conditions were performed by each participant in 16 blocks. These conditions comprised 4 *axes* x 2 *response mappings* x 2 *sensory modalities* (auditory and visual). The 16 blocks were split in four sessions that were performed on four different days. Every session consisted of four blocks, one block with each axis. All four axes were measured with each participant on a given day for one stimulus-response mapping and one sensory modality (auditory and visual). The order of measurements for the axes and response mappings in the first session was pseudorandomly chosen for half of the participants. The other half had the same order of axes, but started with the opposite response mapping. For instance, if subject 1 started with Horizontal axis and “left even” followed by Vertical axis and “up even” etc., subject 2 started with Horizontal axis and “left odd” followed by Vertical axis and “up odd” etc. In the next session, response mappings were switched accordingly. 15 subjects started with the auditory presentation modality, while 13 participants started with the visual presentation modality. One presentation modality was always recorded on two subsequent recording-sessions, but not necessarily on two subsequent days.

A block consisted of various trials. Throughout each trial, participants had to keep their gaze within an invisible, electronically defined circle with a radius of 1.2° centred on the fixation point. Subjects were instructed to move their gaze after stimulus presentation from the fixation point to the correct target (see below). Stimuli were presented pseudorandomly. Trials in which fixation was broken too early were immediately aborted and repeated at the end of the set in pseudorandom order until they were performed appropriately. Trials in which stimulus presentation was erroneous due to technical reasons (framedrops) were repeated in the same way. Every trial was started by the participant by pressing the *spacebar* of the keyboard, thereby re-adjusting the eye-position in the centre of the screen with the Eyelink-recordings (drift-correction). Between 500 ms and 1000 ms after fixation onset, a stimulus (number) was presented and the participant was asked to respond to this number depending on the parity and the stimulus response mapping used in that block of trials. The trial ended 200 ms after the gaze position correctly left an invisible circle with a radius of 4.7° around the fixation point. If no saccades were performed within 2 seconds after stimulus onset, the trial was marked as invalid and repeated at the end of the set in pseudorandom order.

The position of the saccade targets depended on the target axis and could be positioned on either the “Horizontal” (**R–L**), the “Vertical” (**U–D**), the “Diagonal_1:30” (**RU–LD**) or the “Diagonal_4:30” (**RD–LU**) axis. I will use these terms and abbreviations in the following distinguish between the axes. As stated above, data for certain target axes were recorded blockwise. At the beginning of each block the actual response mapping was presented as written instruction (e.g. “links oben gerade – rechts unten ungerade”, German for: “left up even – right down odd”). Each block consisted of 35 repetitions of the eight numbers, resulting in a total of 280 trials. At the beginning of each block, eight practice trials (each number once) were performed to familiarize participants with the current axis and response mapping.

3.5.1.3 Analyses

In a first step, saccades were determined from the eye movement data by a threshold criterion: whenever the speed of the eyes went beyond 80°/s this was considered a saccade. Beginning and end of a saccade (in space and time) were defined as the instances for which the movement first/last reached 20°/s. Reaction time (RT) was defined as time between stimulus onset and saccade onset. As data was recorded from two eyes, the start- and endpoints of the saccade were determined as the mean of both eyes' saccades.

For further analysis of the data, I defined eye-movement target-areas. Since in one block saccade targets were always on opposite sides, only the correct saccade direction had to be determined. Starting in the fixation point and reaching to the saccade target, a target area was defined as triangular having a 90° angle in the fixation point symmetrically positioned around the axis. In general saccades landing inside this area were considered as valid saccades. The following performances were considered invalid trials: (i) saccades which did not start inside a circle with a radius of 1.2° around the fixation point, (ii) saccades which did not land outside a circle with a radius of 4.7° around the fixation point, (iii) saccades that started before stimulus onset as well as (iv) saccades which had binocular gaze-end-position-differences of more than 5° (strabismus). Trials without any saccade, trials with invalid saccades as well as practice trials were excluded from further analysis. Trials with valid saccades to the wrong side were excluded from the main RT-analysis, too, but were taken into account when analysing response accuracy (also called percentage of error-trials (ER)).

In the next step, I tested for the presence of a SNARC effect in each axis and sensory modality. To this end, I applied two different analyses, the classic slope-analysis (c.f. Dehaene et al., 1993) on the one hand and a repeated measures *analysis of variance* (ANOVA) on the other hand. For the slope-analysis I calculated - for each participant, axis and sensory modality individually - the linear regression for the difference between median RTs to the one side minus median RTs to the opposite side for each presented number. In the classical SNARC setting (i.e. answers only to the left and to the right) the RT-difference is calculated as **"right – left" (R–L)**, since the reaction to larger numbers is expected to be faster on the right side. I used the same difference for horizontally measured data (Horizontal). From now on I will use the terms **small-numbers-preferred-side (SNPS)**, which was left in the horizontal case and **large-numbers-preferred-side (LNPS)** which in this case was the right side. "Preferred" in this case expresses the expectation that reactions should be faster or more accurate to this side. For the Vertical axis I assumed a mental number line with higher numbers on the top (Ito & Hatta, 2004; Schwarz & Keus, 2004; Gevers et al., 2006b; Shaki & Fischer, 2012; Hartmann et al., 2014). Therefore, I calculated reaction time differences as **"up – down" (U–D)** (up = LNPS and down = SNPS). The Diagonal_1:30 from the lower left to the upper right was congruent with this two previously reported directions (right up = LNPS and left down = SNPS). Consequently, I calculated **"right up – left down" (RU–LD)**. The fourth axis (Diagonal_4:30), i.e. upper left to the lower right, was incongruent with one of the two axes along the horizontal and the vertical meridian, since large numbers were expected to be responded to faster on the right side and on the upper side. Hence, my assignment **"right down – left up" (RD–LU)** (right down = LNPS and left up = SNPS) was one of two possible solutions, but in line with the assignment chosen by Gevers and colleagues (2006b) and Holmes and Lourenco (2011, 2012). All further analyses were performed with respect to these assignments. For statistical analysis, I performed a single-sided signed-rank test whether or not the median of the regression slopes from all participants within one axis and sensory modality was significantly different from and below zero.

Additionally, I applied a repeated measures three-way ANOVA (c.f. Nuerk et al., 2005) on median RTs, grouped by approximate *magnitude* (i.e. grouping number values 1 & 2 together as one magnitude, as well as 3 & 4, 6 & 7 and 8 & 9), *response side* (SNPS, LNPS) and *parity* (odd, even) as factors. In these tests a SNARC effect would be represented by an interaction between *magnitude* and *response side* along with a negative median slope.

Since the SNARC effect is generally not only visible in reaction times but sometimes also in response accuracy (Schwarz & Keus, 2004; Keus & Schwarz, 2005; Nuerk et al., 2005; but see Wood et al., 2006a), I repeated the two analyses described above acting on the percentage of error-trials (ER) instead of median RT. I calculated the proportion of error-trials as number of trials with answers to the wrong side divided by the number of all valid trials (trials in which correct saccades were detected, see above) individually for each participant and each condition (*magnitude* x *response side* x *parity*).

In order to determine differences in SNARC strength between axes and/or between sensory modalities I applied two additional types of repeated measures ANOVAs. In principle, these ANOVAs were applied as described above, but once separately for each modality with the additional factor *axis* (Horizontal, Vertical, Diagonal_1:30 and Diagonal_4:30) and once in a five-way ANOVA with all conditions taken together using *axis* (as above) and *sensory modality* (auditory, visual) as additional factors. These ANOVAs were supposed to reveal any difference in SNARC strength between axes within one sensory modality and any difference in SNARC strength between sensory modalities, if present.

The central aim of this study was to test for the existence of a frontoparallel "SNARC plane". Therefore, I calculated multiple linear regressions over the calculated slopes (see above) of the cardinal axes (Horizontal and Vertical) to fit the slopes of one diagonal axis (Diagonal_1:30 or Diagonal_4:30). Significant multiple linear regressions would reveal that the regression slopes on reaction time differences along the diagonal axes could be described as a linear superposition of the regression slopes on reaction time differences along the cardinal axes and would hence provide evidence for the existence of a frontoparallel SNARC plane.

3.5.2 Results

Behavioural results were obtained from 28 participants performing a total amount of 62,720 trials for each sensory modality. In the auditory modality, 4,442 trials (7.1%) were not considered for further analysis because (i) saccades were either invalid (855 trials, 1.4%) or because (ii) response behaviour was not correct (3,587 trials, 5.7%, see chapter 3.5.1.3 Analyses for details), leaving 58,278 trials for an in-depth analysis. In the visual modality 5,744 trials (9.2%) were not considered for further analysis ((i): 1,237 trials (2.0%) and (ii): 4,507 trials (7.2%)) leaving 56,976 trials. Considering the different conditions (*magnitude* x *parity* x *response side* x *axis* x *sensory modality*) each participant performed on average 32.2 (std: 2.8) of the 35 trials correctly (auditory: mean: 32.5 (std: 2.7), visual: mean: 31.8 (std: 3.0)). These trials were further analysed.

Mean reaction times (RT) were 390.4 ms (visual modality) and 535.4 ms (auditory modality), respectively. RTs between sensory modalities differed significantly (two sample double-sided t-test: $t(0.95; 105090) < -189$, $p < .0001$). In the auditory modality, mean RTs for the different axes were as follows: R–L: 533.5 ms, U–L: 546.9 ms, RU–LD: 538.3 ms and RD–LU: 522.9 ms. RTs were not significantly different (repeated measures ANOVA, $F(3,81) = 1.37$, $p > .25$). In the visual modality, the respective values were: R–L: 389.6 ms, U–L: 394.9 ms, RU–LD: 389.5 ms and RD–LU: 387.6 ms. Again, differences in RTs were not statistically significant (repeated measures ANOVA, $F(3,81) = 0.45$, $p > .7$). See Appendix B1 (chapter 6.3) for a detailed list of all averaged RTs.

3.5.2.1 SNARC Effect in Different Conditions

To determine in which axes and sensory modalities a SNARC effect was present, I calculated the difference between median RTs for answers to the side that was expected to be preferred for answers to large numbers and median RTs for answers to the opposite side (LNPS–SNPS) individually for each number, axis, sensory modality and participant. Then I calculated a linear regression for these differences as a function of number, again separately for axes, sensory modalities and participants. In a final step, I computed a single-sided singed-rank test over slopes from all participants in order to determine whether or not these slopes were significantly different from and below zero. For the visual modality, the slopes of the Horizontal axis ($p = .041$) and of Diagonal_1:30 ($p = .0001$) were significantly different from zero (see Figure 3-6). The slopes of the Vertical axis ($p = .078$) and the Diagonal_4:30 ($p = .093$) were close to significant and revealed a trend. In the auditory modality all tests were not significant (all $p > .16$).

The slopes, calculated over percent errors (ER), showed a significant SNARC effect in the visual modality for three out of four axes (all $p < .02$), but not for Diagonal_4:30 ($p = .48$) (see Figure 3-7). For the auditory modality the Diagonal_1:30 showed a significant SNARC effect (p = .0015) and the Vertical axis revealed a trend (p = .069). The slopes in the other two axes were not significantly negative (all p > .36).

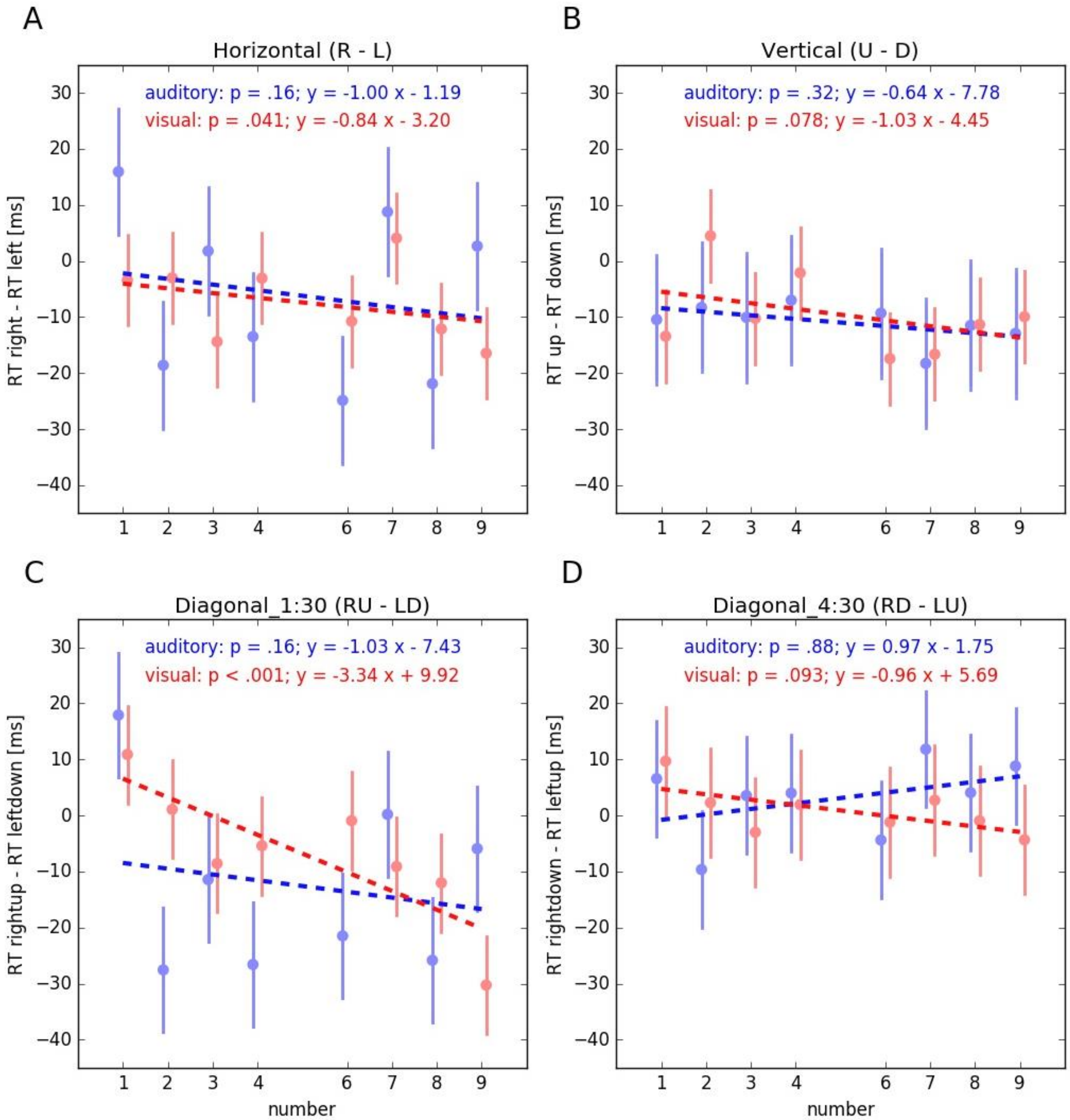


Figure 3-6: Differences in median reaction time (RT) between responses on the "large numbers preferred side" (LNPS) and on the "small numbers preferred side" (SNPS) for each number averaged across participants (error bars indicate standard error of the mean) plotted for cardinal (A and B) and diagonal (C and D) axes. The auditory modality is presented in blue while the visual modality is presented in red. Data points are slightly shifted with respect to each other along the abscissa to allow for a comparison. In this graphical regime, a SNARC effect is indicated by a larger difference for low numbers and a smaller difference for high numbers and, hence, results in a negative slope of a linear regression (dashed line). The SNARC effect is significant only for Horizontal axis and Diagonal_1:30 in visual modality (single-sided signed-rank test). Vertical axis and Diagonal_4:30 in visual modality show a trend.

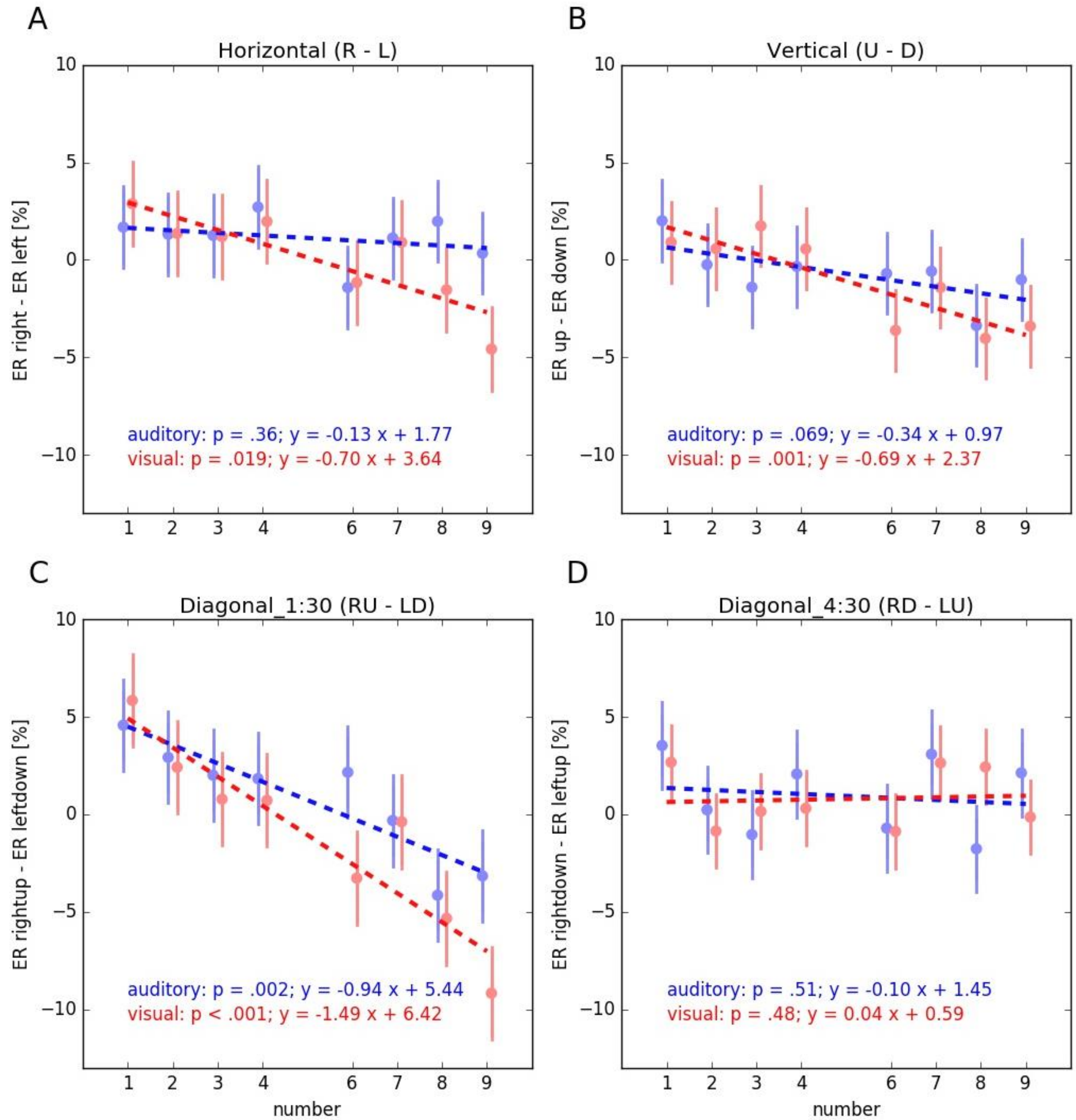


Figure 3-7: Differences in percent response error (ER) between responses on the "large numbers preferred side" (LNPS) and on the "small numbers preferred side" (SNPS) for each number averaged across participants (error bars indicate standard error of the mean) plotted for cardinal (A and B) and diagonal (C and D) axes. The auditory modality is presented in blue, while the visual modality is presented in red. Data points are slightly shifted with respect to each other along the abscissa to allow for a comparison. In this graphical regime, a SNARC effect is indicated by a larger difference for low numbers and a smaller difference for high numbers and, hence, results in a negative slope of a linear regression (dashed line). In visual modality the SNARC effect is significant for the two cardinal axes and the Diagonal_1:30 (single-sided signed-rank test). In auditory modality the SNARC effect is significant for Diagonal_1:30 and shows a trend for the Vertical axis.

In the repeated measures ANOVAs, as determined on median RTs for each condition separately, with the factors *magnitude*, *response side* and *parity*, a SNARC effect would be represented by a significant interaction of *magnitude* x *response side*. Such a significant interaction occurred in the visual modality for Diagonal_1:30 ($F(3,27) = 9.76$, $p < .00001$). Furthermore, a trend for the Horizontal axis in the visual modality ($F(3,27) = 2.63$, $p = .056$) was present. In combination with the negative mean slopes (Diagonal_1:30: –3.34 ms/number; Horizontal axis: –0.84 ms/number) this indicated the presence of a SNARC effect. For the repeated measures ANOVAs as applied to response accuracy values I found one significant interaction (*magnitude* x *response side*) in the auditory modality (Diagonal_1:30: $F(3,27) = 7.67$, $p = .0001$) and three significant interactions in the visual modality (Horizontal axis: $F(3,27) = 2.75$, $p = .048$; Vertical axis: $F(3,27) = 4.22$, $p = .008$; Diagonal_1:30: $F(3,27) = 12.33$, $p < .00001$). Together with the negative mean slopes (auditory Diagonal_1:30: –0.94 ms/number; visual Horizontal axis: –0.7 ms/number; visual Vertical axis: –0.69 ms/number; visual Diagonal_1:30: –1.49 ms/number) these findings indicated a significant SNARC effect in these conditions.

Different main effects and interactions reached significance, too. A detailed summary of p-values is listed in Appendix B2 (see chapter 6.4). Notably I did not find any significant interaction of *response side* x *parity*. Such an interaction would have been indicative of a MARC effect (linguistic <u>ma</u>rkedness of <u>r</u>esponse <u>c</u>odes; Nuerk et al., 2004, see chapter 2.1.2.2 The MARC Effect) in my data (all $F(1,27) < 3.35$, $p >. 078$). Behaviourally, a MARC effect would have led to faster right side responses to even digits and faster left side responses to odd digits.

3.5.2.2 Differences Between Sensory Modalities and Orientations

Figure 3-6 and Figure 3-7 show the difference in the strength of the SNARC effect between axes and sensory modalities. Statistically these data were tested with a five-way repeated measures ANOVA with factors *axes* (Horizontal axis, Vertical axis, Diagonal_1:30, Diagonal_4:30) and *sensory modality* (auditory, visual) in addition to the factors used before (*magnitude*, *parity*, *response side*). As before a significant interaction *magnitude* x *response side* would indicate a SNARC effect. The ANOVAs revealed such a significant interaction for RTs ($F(3,81) = 4.02$, $p = .01$) and ERs ($F(3,81) = 9.27$, $p < .0001$) indicating a global SNARC effect in my data. Furthermore, an interaction *magnitude* x *response side* x *axis* was present for RTs ($F(9,243) = 2.61$, $p = .007$) and ERs ($F(9,243) = 3.95$, $p = .0001$), indicating differences in SNARC strength between axes. For RTs also an interaction *magnitude* x *response side* x *sensory modality* was significant ($F(3,81) = 2.84$, $p = .043$), indicating differences in SNARC strength between auditory and visual presentation.

Finally, in order to further quantify the differences between axes, I computed repeated measures ANOVAs within each sensory modality, having *magnitude*, *parity*, *response side* and *axis* as factors. The interaction *magnitude* x *response side* was significant for visual modality (for RTs and ERs) and for ERs in auditory modality (all $F(3,81) > 3.7$, $p < .015$), but not for RTs in auditory modality. The interaction *magnitude* x *response side* x *axis* again was significant for the first three mentioned conditions (all $F(9,243) > 2.18$, $p <. 024$), but not for the fourth. This result indicates that in sensory modalities, where a SNARC effect was present, the SNARC effect differed significantly between axes.

3.5.2.3 SNARC-Slope-Superposition of Cardinal Axes to Diagonal Axes

The major goal of this study was to compare the SNARC effect on cardinal axes with the SNARC effect on diagonal axes in the same subjects. Therefore, I used the calculated regression slopes (see chapter 3.5.1.3 Analyses) as an indicator of SNARC strength. In order to test for a superposition of a SNARC effect along the horizontal and the vertical axes towards a 2-D SNARC plane, I calculated multiple linear regressions using the slopes for the cardinal axes (Horizontal and Vertical) as predictor of the slopes on the diagonal axis (Diagonal_1:30 or Diagonal_4:30). I repeated this analysis for RTs and ERs in both sensory modalities resulting in eight multiple linear regressions. Results of this multiple regressions can be found in Table 3-2. For response accuracy three of the four regressions were significant and the fourth regression (visual Diagonal_1:30) showed a close to significant trend. For RTs a significant regression was found in half of the cases (auditory Diagonal_1:30 and visual Diagnonal_4:30).

Table 3-2: Results of the multiple linear regressions in auditory and visual modality for Diagonal_1:30 (RU–LD) and Diagonal_4:30 (RD–LU). Regressions were done with the slopes calculated for the cardinal axes (Horizontal and Vertical) as predictors. Regression coefficients show the weight that was applied to the predictors (including a constant term "const.") to obtain the regression. The p-values of significant regressions are grey-shaded.

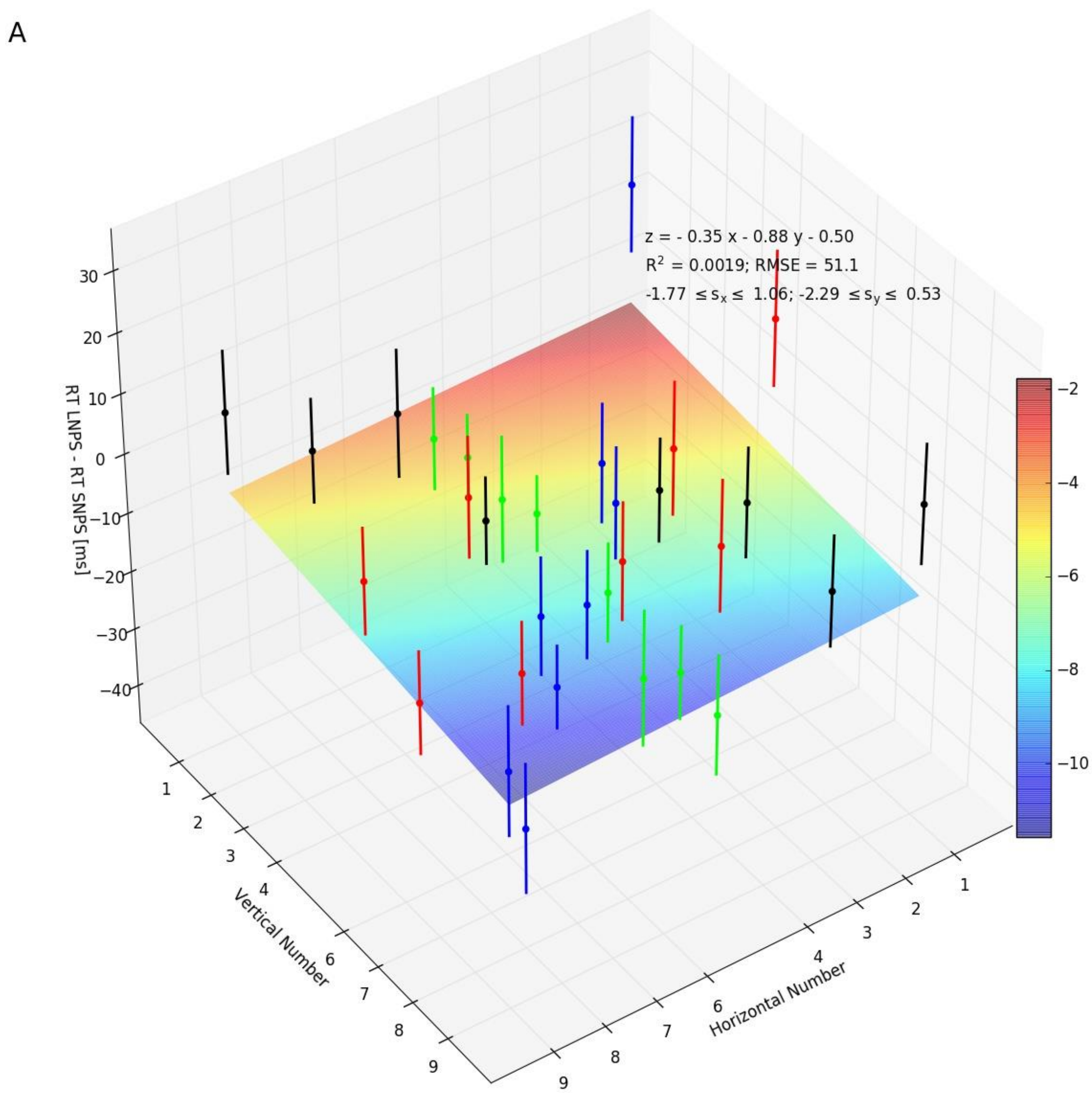
	condition		statistical values		regression coefficients		
	modality	Diagonal	p	R^2	const.	Horizontal	Vertical
RT	auditory	1:30	.033	.24	–0.35	0.43	0.39
		4:30	.65	.03	1.12	0.16	–0.02
	visual	1:30	.37	.08	–3.13	0.30	–0.04
		4:30	.049	.21	–1.07	0.29	–0.35
ER	auditory	1:30	.003	.37	–0.70	0.41	0.56
		4:30	.002	.40	0.00	0.50	0.10
	visual	1:30	.053	.21	–0.95	0.43	0.34
		4:30	.028	.25	0.06	0.30	–0.28

In addition to this multiple regression analysis, I also displayed the RT-differences (ER-differences, respectively) in a three-dimensional plot: with the presented number in horizontal and vertical orientation as independent variable and the measured differences on the four axes as dependent variable. I fitted a 2-D plane to these data points (see Figure 3-8 and Table 3-3 for parameters). Since the 2-D plane was the 3-D equivalent of the classical SNARC regression slope, a negative plane slope (in x- and/or y-orientation) would indicate a SNARC effect in the corresponding axis. The significance of these plane-slope-parameters would be confirmed if the 95% confidence interval of the parameter was negative, since in such case the slope was negative with $p < .05$. For ER-differences

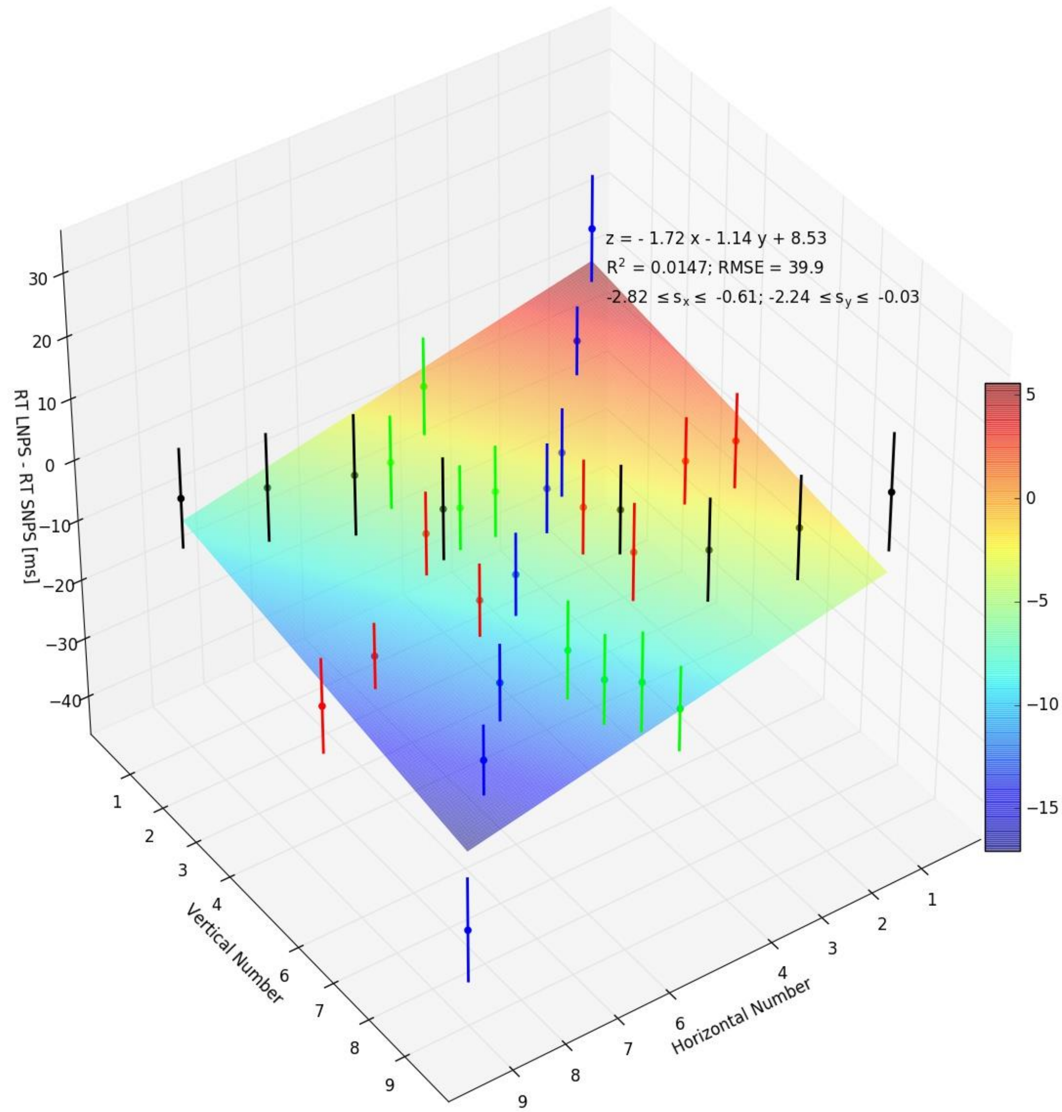
Table 3-3: Results of the fit on RT- and ER-differences in 3-dimensional space (see Figure 3-8). Fit was done with the regression-function $f(X,Y) = s_x * X + s_y * Y + c$. Upper and lower bound of the corresponding 95%-confidence interval is listed in "min" and "max" columns. For slope-parameters "s_x" and "s_y" these confidence intervals indicate a significant SNARC effect in the corresponding cardinal axis if both values are negative, which is the case in all conditions except for auditory RTs.

		s_x			s_y			c			stats.	
		min	s_x	max	min	s_y	max	min	c	max	R^2	RMSE
RT	aud	–1.77	–0.35	1.06	–2.29	–0.88	0.53	–11.0	–0.5	10.0	.002	51.10
	vis	–2.82	–1.71	–0.61	–2.24	–1.14	–0.03	8.5	0.3	16.8	.015	39.90
ER	aud	–0.61	–0.39	–0.17	–0.61	–0.39	–0.17	2.8	4.4	6.1	.027	7.87
	vis	–0.97	–0.72	–0.46	–1.00	–0.74	–0.49	5.1	7.0	8.9	.066	9.20

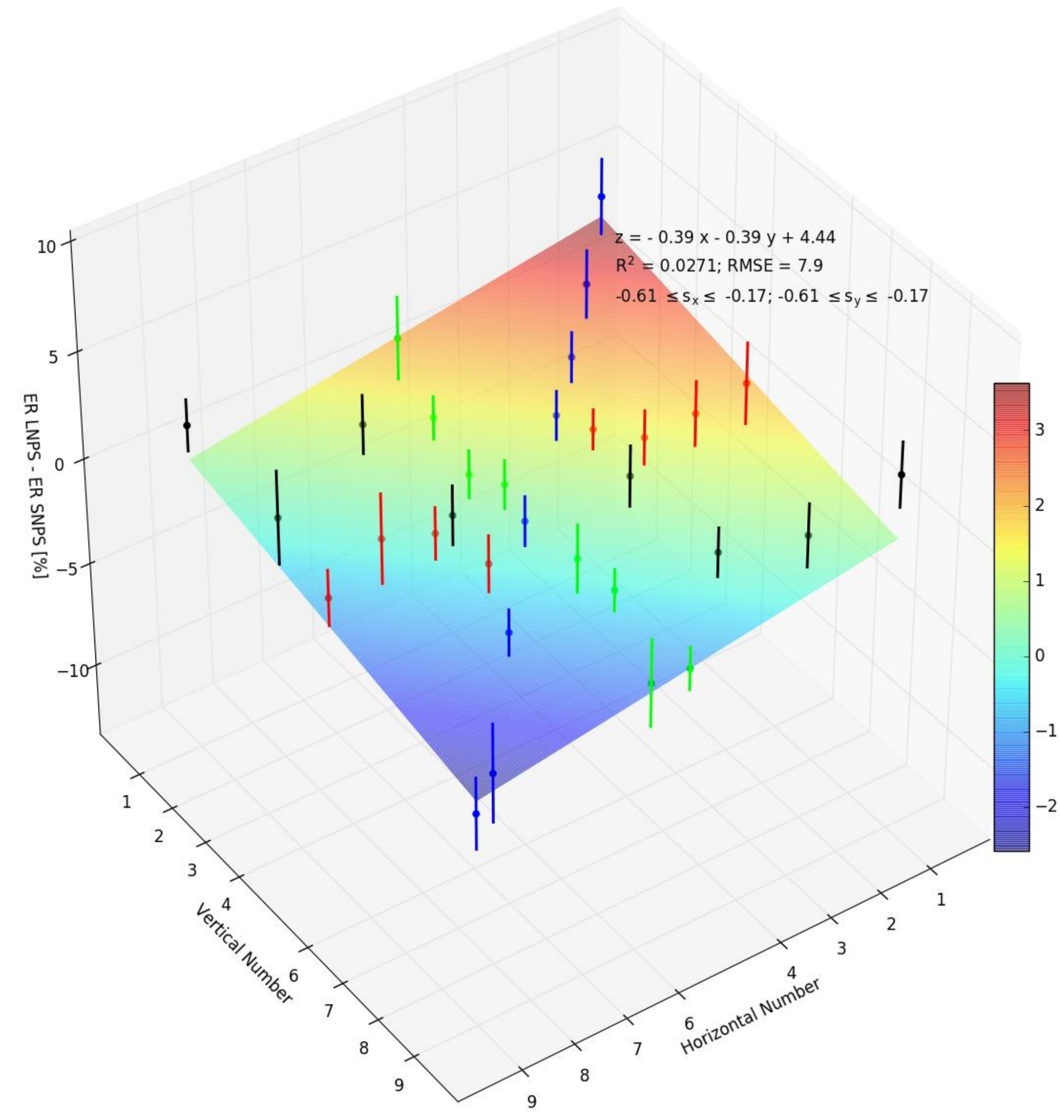
the 95% confidence intervals of the fitted plane-slope-parameters were all below zero, confirming the above found significant SNARC effect. For RT-differences in the visual modality the confidence intervals were negative as well. The confidence intervals of the auditory RT-differences were positive on one side of the interval and negative on the other, leading to no conclusive result.



B


z = - 1.72 x - 1.14 y + 8.53
R^2 = 0.0147; RMSE = 39.9
-2.82 ≤ s_x ≤ -0.61; -2.24 ≤ s_y ≤ -0.03
RT LNPS - RT SNPS [ms]
Vertical Number
Horizontal Number

C



z = - 0.39 x - 0.39 y + 4.44
R² = 0.0271; RMSE = 7.9
-0.61 ≤ sx ≤ -0.17; -0.61 ≤ sy ≤ -0.17
ER LNPS - ER SNPS [%]
10
5
0
−5
−10
Vertical Number
1
2
3
4
6
7
8
9
Horizontal Number
1
2
3
4
6
7
8
9
3
2
1
0
−1
−2

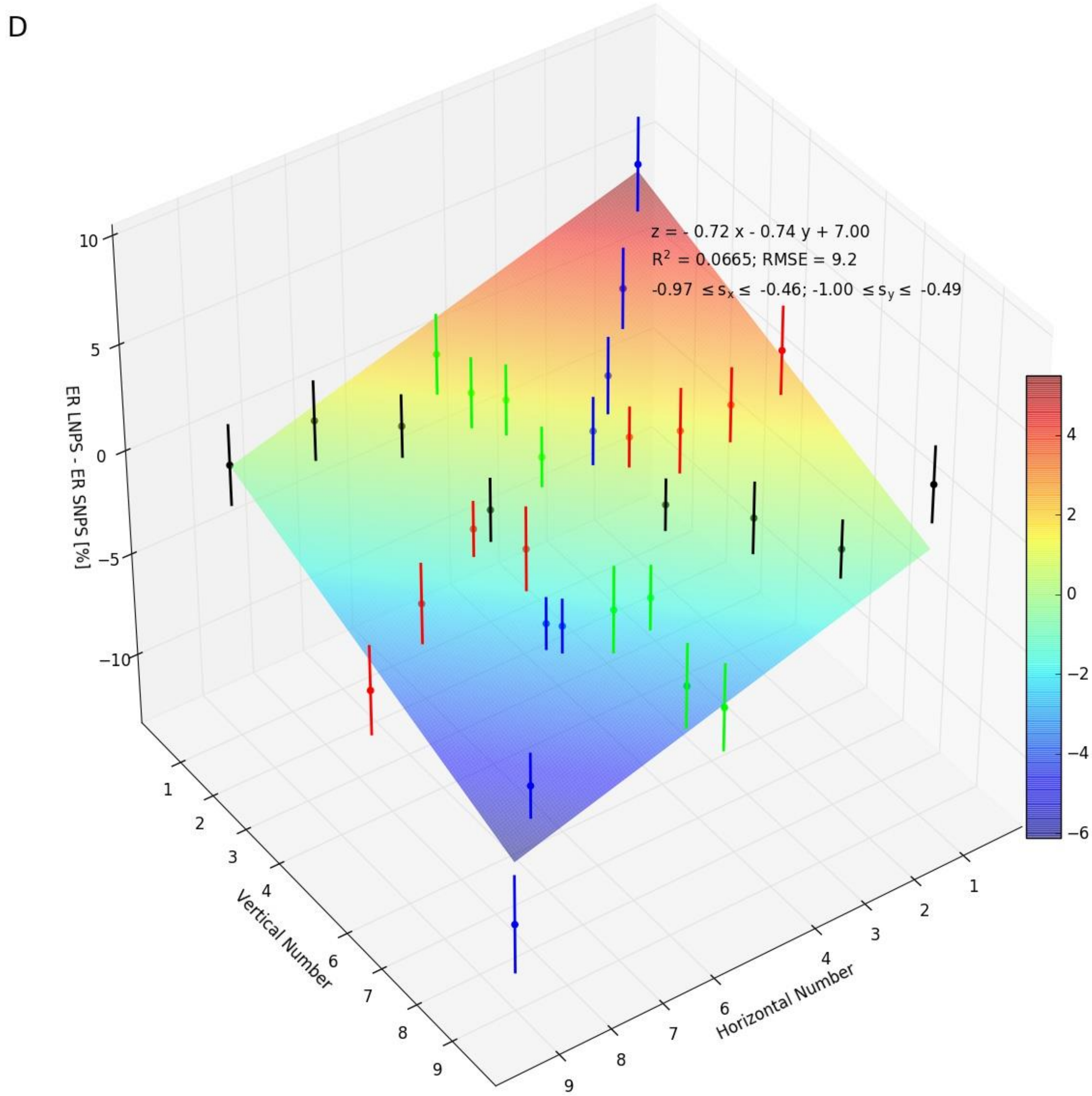


Figure 3-8: Three-dimensional presentation of the differences in median reaction time (RT) (A and B) and the response accuracy (ER) (C and D) between responses on the "large numbers preferred side" (LNPS) and on the "small numbers preferred side" (SNPS) for each number averaged across participants (error bars indicate standard error of the mean) for auditory (A and C) and visual (B and D) modality. X- and Y-position is determined by the presented number and the axis of the measured condition (note that plot axes are reversed for a better presentation). Data of Horizontal axis is shown in red, Vertical axis is shown in green, Diagnonal_1:30 is shown in blue and Diagonal_4:30 is shown in black. The fitted plane is the three-dimensional equivalent of the two-dimensional SNARC-regression-slope (see Figure 3-6 and Figure 3-7) and hence, indicating a two-dimensional SNARC effect if significantly negative in both slope-parameters. This is the case for B, C and D, since both 95%-confidence intervals are negative.

3.5.3 Discussion

I performed a SNARC experiment with 28 participants using saccadic eye movements as responses. Answers were given along four different axes (Horizontal, Vertical, Diagonal_1:30 and Diagonal_4:30) and for two stimulus modalities (auditory and visual). The goal of this study was to compare, within individual subjects, the SNARC effect across different axes and sensory modalities.

3.5.3.1 Evidences for a Frontoparallel SNARC Plane

My findings confirm the conclusions drawn by Gevers and colleagues (2006b). They investigated the SNARC effect on the diagonals solely with button presses on a horizontally orientated keyboard. The authors found a significant SNARC effect on the “right-diagonal” (named Diagonal_1:30 in my study) but no SNARC effect on the “left-diagonal” (Diagonal_4:30). They concluded a superposition of the cardinal axes from these findings, since on Diagonal_4:30 the orientation of the SNARC effect for two cardinal axes were opposite to each other. Many of my findings support this conclusion and extend it to saccadic responses in the frontoparallel plane, as hypothesized by Schwarz and Keus (2004). In contrast, my data are not in line with the idea proposed by Holmes and Lourenco (2011, 2012) that the vertical SNARC effect would only be a realigned horizontal SNARC effect.

The first indication for my hypothesis of a frontoparellel SNARC plane is that my results for ER were very similar to the results reported by Gevers and colleagues (2006b). In both sensory modalities (auditory and visual) I received a strong significant SNARC effect on the Diagonal_1:30 and no significant SNARC effect on the Diagonal_4:30, which is in line with their previously published RT- and ER-results.

A second indication for my hypothesis is yield by the five-way ANOVAs that showed a global SNARC effect in my data (for RTs and ERs) but also significant differences for the SNARC effect between different axes. The four-way ANOVAs proofed that this pattern arose not only from the visual modality, but was also present in accuracy data for auditory modality. For a superposition of SNARC behaviour on the cardinal axes to SNARC behaviour on the diagonal axes, as stated by Schwarz and Keus (2004) and Gevers and colleagues (2006b), differences between axes are mandatory.

The third and most important indication for the interaction of the cardinal axes on the diagonal axes, and hence the existence of a SNARC plane, are the significant multiple regressions. Different from previous studies, which have tested for a SNARC effect only for the cardinal or only for the diagonal axes, I was able to test for a superposition of effects since I tested subjects for all four axes. My results unequivocally show that the regression slopes of the SNARC effect on the diagonal axes can be predicted by a linear superposition of the regression slopes of the SNARC effect on the cardinal axes. Furthermore, when looking at the regression coefficients of the significant visual regressions (see Table 3-2), it was noticeable that the coefficient for the Vertical axis was negative for Diagonal_4:30 while the coefficient for the Horizontal axis was positive. This change of sign could be explained by the chosen (see chapter 3.5.1.3 Analyses) assignment “right down – left up” that was in contrast to the assignment “up – down” on the Vertical axis. Hence, the SNARC effect on the vertical axis had to be reversed to fit for this diagonal. The coefficients for the other close to significant multiple linear regression on ER-data on Diagonal_1:30 in visual modality did not have such a change of sign. The regression for Diagonal_1:30 on visual RT-data did not reach significance so that no conclusions could be drawn out of it. This might be caused by the relatively weak SNARC effect in Vertical orientation. Taken together these are very strong evidences for the existence of a *mental number plane*, at least for saccadic responses, where large numbers are represented in the upper right, and small numbers are represented in the lower left, just as presented in Figure 3-8.

One could argue that it might be the case that the assumptions by Holmes and Lourenco (2011, 2012) were correct and the vertical SNARC effect was just a result of a highly dominant horizontal SNARC effect that was adapted for vertical axis. I indeed found just a weak vertical SNARC effect (a close to significant trend) in RT-data and not a significant one as expected (Schwarz & Keus, 2004). But this was in contrast to the findings from Holmes and Lourenco (2011, 2012) who reported a nonsignificant <u>inverted</u> SNARC effect on the vertical axis. Furthermore, the vertical SNARC effect in my ER-data was not only significant but SNARC strength (regression slope) was rather equal in horizontal and vertical condition. Additionally I could not find an “overrulement” of the horizontal axis over the vertical axis. If there had been such an “overrulement” of the horizontal axis on the vertical axis, a significant SNARC effect on Diagonal_4:30 would have been expected, since on this axis the vertical axis was incongruent with the SNARC analysis (see chapter 3.5.1.3 Analyses). In contrast to that no SNARC effect was found (slope near zero), as would have been expected from a homogeneous superposition. Unfortunately Holmes and Lourenco reported no results on response accuracy analysis so that comparisons are not possible.

Another indication of the equality of the two cardinal axes was provided by the computed weights in the multiple linear regressions. If the horizontal axis would have had a major impact on the diagonal axes, the expected weight for the horizontal axis should have been much higher than the expected weight for the vertical axis. If one neglects the sign and concentrates on the absolute values (which is adequate, since the change in sign reflects the reversed orientation of the vertical axis in Diagonal_4:30 as described above) the weights have approximately the same amount and no tendency for bigger values on the horizontal axis. Therefore, I still argue that my results point towards the existence of a mental number plane and not on a “horizontal trump”.

Besides the concept of the *mental number line* (MNL), an alternative explanation for the SNARC effect has been proposed, the *polarity correspondence principle* (Proctor & Cho, 2006; but see Santiago & Lakens, 2013; see chapter 2.1.2.1 The SNARC Effect – polarity correspondence principle). This account refers to the idea that the SNARC effect is not obtained due to the existence of a mental number line, but due to the polarity congruence of a different categories. According to this account the polarity of large numbers is [+] and the polarity of small numbers is [–]. The different response times obtained by a SNARC effect would therefore be a result of the congruent polarity of response side (right [+]; left [–]) and number size. Since the polarity of up ([+]) and down ([–]) (Proctor & Cho, 2006) is also in line with the predicted mental number line orientation on the vertical axis (e.g. Schwarz & Keus 2004; Hartmann et al., 2014) my experimental conditions could not distinguish between those two alternative approaches. However recent studies showed a

SNARC effect even with centrally presented stimuli and centrally given responses (Fischer & Shaki, 2016). Additionally the SNARC effect did not occur for vocal answers “bad” ([–]) and “good” ([+]), while it did occur for answers “left” and “right” (Leth-Steensen & Citta, 2016). Both effects cannot be explained by the polarity correspondence principle but point to a MNL interpretation.

Some caveats on potential confounds have been stated regarding the comparison of horizontal and vertical SNARC effect in general and the measurement of this effect with saccadic eye movements in particular (see Holmes & Lourenco, 2011, 2012; Winter et al., 2015). One potential confound might be raised due to the asymmetry of space in the real world. In fact the extent of rooms is usually bigger in horizontal than in vertical dimension and hence human’s 3-D-search-field has a much larger extend in the horizontal than in the vertical domain. This was also reflected in the size of my screen, which was 120 cm wide but only 90 cm high. This might have led to a confound in participant’s behaviour on the vertical axis. However, I consider this as unlikely since the distance from fixation point to saccade target was the same for both cardinal axes. Another objection raised by Holmes and Lourenco (2011, 2012) was that upward saccades were found to be generally accomplished with less speed than downward saccades (Collewijn et al., 1988). The conclusion that this might influence the vertical or diagonal SNARC effect measured with saccadic responses was inappropriate. The reason is that any effect on differences between upward and downward eye movements were extinguished in the linear-regression analysis with the calculation of the difference. Since the analysis of the SNARC effect was based on regression slopes on the differences (Up – Down) in RT or ER no effect on response side was taken into account. This is also true for both diagonal axes. However, it might still be that differences between my findings and those from Holmes and Lourenco (2012, 2012) were elicited by the difference in the used effector (see chapter 3.4 Study I: The SNARC Effect in Different Effectors).

Finally one could ask whether a “diagonal number representation” makes sense in the real world. “*Numbers are generally not presented diagonally or grid-like in our culture, but instead, aligned either horizontally or vertically (e.g., bar plots, menu prices lists, etc.).*

Children, for example, learn numbers on the number line before they learn the Cartesian coordinate system." (Winter et al., 2015, section 4.1). The fact that, even without this external priming and even without implicit priming before the experiment (c.f. Holmes & Lourenco, 2011, 2012), participants in my study showed a diagonal SNARC effect is remarkable. Even more remarkable is that this diagonal SNARC effect could significantly be described as superposition of the SNARC effect on the cardinal axes. Hence, the organization of numbers on a mental number plane seems not only to rely on "learned behaviour", but might be an intrinsic organization mechanism in the human brain. Hoffmann and colleagues (2013) reported that children aged five and a half years (which means in preschool age) showed a SNARC effect. It would be interesting to test whether young infants might also show this mental number plane.

Taken together my results of a frontoparallel mental number plane and the results by Gevers and colleagues (2006b) who reported a strong SNARC effect on the diagonal "right up – left down" and the results by Chen and colleagues (2015) who suggested a number mapping on the whole transverse plane, lead to the idea of a mental number space (also hypothesized by Chen et al., 2015). In such a space large numbers are represented *right / up / far* and small numbers are represented *left / down / near*. One possible experiment to prove this idea could be repeating my experiment with saccadic responses for all three cardinal axes (abscissa, ordinate and applicate) and the associated diagonals in 3D-space. For this experiment of course a setup with visual stereotopic presentation in combination with eye movement detection would be mandatory. The results of such an experiment should show that the SNARC slopes on the cardinal axes may be combined to the results of any diagonal axis.

3.5.3.2 Differences in SNARC Effect Between Sensory Modalities

The finding that the SNARC effect is amodal (Nuerk et al., 2005), indicating that a SNARC effect is independent from the way numbers are presented (e.g. Arabic numbers, dice patterns, written number words and auditorily presented number words) has already been challenged by Wood and colleagues (2006b) who did not find a significant correlation between auditory stimulus presentation and any (of three) visual stimulus presentations. My data revealed a difference between the auditory and visual modalities, too (see Figure 3-6 and Figure 3-7). This difference was confirmed by the five-way repeated measures ANOVA on RTs revealing a significant interaction between *magnitude* x *response side* x *sensory modality*. This interaction indicated differences in SNARC effect strength (*magnitude* x *response side*) between sensory modalities. Hence, these results prove the difference in the SNARC effect between auditory and (at least one) visual stimulus presentation (Arabic digits). The fact that the SNARC effect was weaker in auditory modality, is also reflected in the response accuracy where a significant SNARC effect was present in Diagonal_1:30 only which is supposed to be the orientation with the strongest SNARC effect (see chapter 3.5.3.1 Evidences for a Frontoparallel SNARC Plane).

A difference between my experimental setting and the measurements performed by Nuerk and colleagues (2005), who claimed the SNARC effect to be amodal, was that those measurements were done with bimanual responses (button presses), while in my experiment participants had to perform saccades. This difference might be of critical importance as my first study has shown that the SNARC effect is effector-dependent (see chapter 3.4 Study I: The SNARC Effect in Different Effectors).

3.6 Study III: Pre-Attentive Processing of Numerical Visual Information

3.6.1 Introduction

The "sense" of numerosity judgement is of critical importance for humans in their everyday life. A neural representation of numerosity has been reported in monkey's intraparietal sulcus and prefrontal cortex (Nieder et al., 2002, 2006; Roitman et al., 2007; Viswanathan & Nieder, 2013), suggesting an evolutionary benefit for the ability of numerosity judgment. In the human brain most numbers are represented by the *approximate number system* (ANS) which has been located bilaterally in the horizontal segment of the intraparietal sulcus by means of functional magneto resonance imaging (fMRI) and electroencephalography (EGG) (Dehaene, 1996; Chochon et al., 1999; Pinel et al., 2001). Numerosity has also been investigated with EEG. Here a decreasing N2 amplitude with an increasing number of presented dots has been shown for values 1 to 9 (Libertus et al., 2007). Furthermore, a modulation of the P2p-component (175 ms to 250 ms) for large numbers has been reported (Hyde & Spelke, 2009). Up to date it is still under discussion whether perception of numerosity is "low-level feature like", as proposed by Burr and Ross (2008), comparable for example to the perception of colour or orientation of stimuli. It is known that numbers up to four are processed not only by the ANS but also by the *object tracking system* (OTS) that allows humans "instantaneously" to judge the amount of very few items (Trick & Pylyshyn, 1994; Feigenson et al., 2002). This effect is called *subitizing*. Due to the detection speed subitizing was often assumed to be pre-attentive (Trick & Pylyshyn, 1993, 1994; Pylyshyn, 2001), i.e. without voluntary or involuntary attention paid to the perceived stimulus. But more recent studies (Railo et al., 2008; Olivers & Watson, 2008; Anobile et al., 2012) showed that, in contrast to processes in the ANS, subitizing was influenced by attentional load.

Pre-attentive perception might be an indication of evolutionary importance, since one can concentrate (or pay attention) on something else and still perceive changes in the relevant domain. One way to detect pre-attentive perception is *mismatch negativity* (MMN) in EEG. MMN describes the phenomenon that *event-related potentials* (ERPs) differ, when within a sequence of equal stimuli (called standards) a deviant stimulus occurs. Typically, ERP-amplitudes around the N2-component (100 ms to 250 ms) evoked by the standard stimuli are less negative than ERP-amplitudes elicited by deviant stimuli. At first, MMN has been demonstrated for auditory stimuli (Näätänen et al., 1978) and has been found for different stimulus features among them: frequency, loudness (e.g. Näätänen et al., 1978), duration (e.g. Jacobson & Schröger, 2003) and recently numerosity (Ruusuvirta & Astikainen, 2016). MMN could be observed even when participants were engaged in a difficult task drawing attention off the stimulus (see Sussman, 2007 for a review). Therefore, MMN is commonly seen as an evidence for pre-attentive perception.

In addition to the auditory mismatch negativity (MMN), MMN has also been demonstrated for visual stimuli (see Kimura, 2012 for a review). Visual mismatch negativity (vMMN) was found for several visual features, such as colour (e.g. Czigler & Sulykos, 2010; Müller et al., 2010), size (e.g. Kimura et al., 2008a), orientation (e.g. Astikainen et al., 2008; Czigler & Sulykos, 2010; Kimura et al., 2010b), location (e.g. Berti, 2009), shape (e.g. Bubrovszky & Thomas, 2011), luminance/contrast (e.g. Kimura et al., 2008b), spatial frequency (e.g. Kenemans et al., 2003), direction of motion (e.g. Pazo-Alvarez et al., 2004; Amenedo et al., 2007), duration (e.g. Qiu et al., 2011) and facial expression (e.g. Zhao & Li, 2006). To the best of my knowledge, vMMN has not yet been demonstrated for numerosity.

Due to the importance of numerosity detection especially in the subitizing range, I proposed visual MMN in the subitizing range. In order to test my hypothesis, I presented visual stimuli, consisting of a certain number of circular patches (1, 2 or 3), to participants of my study. As in classical MMN paradigms a standard was presented frequently, interrupted by an infrequent deviant. Stimuli were presented laterally to a central fixation point and subjects were engaged in a difficult foveal detection task guiding their attention off the number stimuli. Results unequivocally revealed the presence of a visual MMN for numerosity changes. Hence, my study provides further evidence for the idea that the processing of numerical information in the subitizing range is pre-attentive.

3.6.2 Methods

3.6.2.1 Participants

A total of ten participants (five male) aged between 22 and 30 (mean 26.9) were recruited from the university population. All participants had normal or corrected to normal vision. All participants except two (subject I, the author and subject II) were naïve about the purpose of the study and were compensated with 8 € per hour for participation. After completing the full experiment each interested participant was given full disclosure on the purpose of the experiment. Participants provided written informed consent before commencing the experiment and all procedures were approved by the local ethics committee and were in agreement with the Declaration of Helsinki.

3.6.2.2 Setup

Experiments were performed in a dark, sound attenuated and electrically shielded room. Participants sat on a chair resting their heads on a chin rest placed centrally in front of a screen. The distance between the screen and the participants' eyes was 68 cm. The screen was a 52 cm (41.8°) wide and 29.25 cm (24.3°) high TFT monitor (ViewPixx/3D Lite, VPixx Technologies Inc., Saint-Bruno, QC, Canada). The resolution of the screen was set to 1920 x 1080 pixels and the refresh rate to 100 Hz. By employing the monitor's *scanning-backlight-mode* the behaviour of a CRT screen was simulated. Stimulus presentation was controlled by the Psychophysics Toolbox 3. EEG was recorded continuously (sample rate: 1000 Hz) using 64 Ag/AgCl active electrodes (Brain Products GmbH, Gilching, Germany). Electrode scalp locations were conform to the *extended international 10 - 20 system* (see chapter 2.3.2 Hardware Setup). Electrode impedance was kept below 5 kΩ. EEG signals were recorded with Brain Vison PyCorder. Participants' right eye position was recorded with an EyeLink 1000Plus (SR Research Ltd., Ottawa, Canada) at a sampling rate of 1000 Hz and further processed as additional EEG-channels (horizontal and vertical gaze position on the screen).

3.6.2.3 Stimuli

A black fixation point (luminance: 0.2 cd/m²; radius: 0.11°) in the middle of a grey screen (luminance: 8.6 cd/m²) was displayed throughout all trials. As task-target a small 0.03° thick ring (radius 0.14°) coloured in darkly grey (luminance: 1 cd/m²) was displayed around the fixation point. Task unrelated stimuli consisted of one, two or three white circular patches (luminance: 62 cd/m²). Patches could be presented either in the left or the right part of the visual field and had either the same radius or same total area, so that either patch size (hereafter called "SizeCon") or total luminance (hereafter called "LumCon") was conserved (for a comparison of the different conditions see Figure 3-9). In the following I will use the terms "Right" and "Left" to refer to the condition in which the stimuli were presented in the right part of the visual field, or in the left part, respectively. X and Y coordinates of the centre of the patches within a visual hemifield were beforehand pseudorandomly chosen (from a uniform distribution) within an imaginary circle with radius

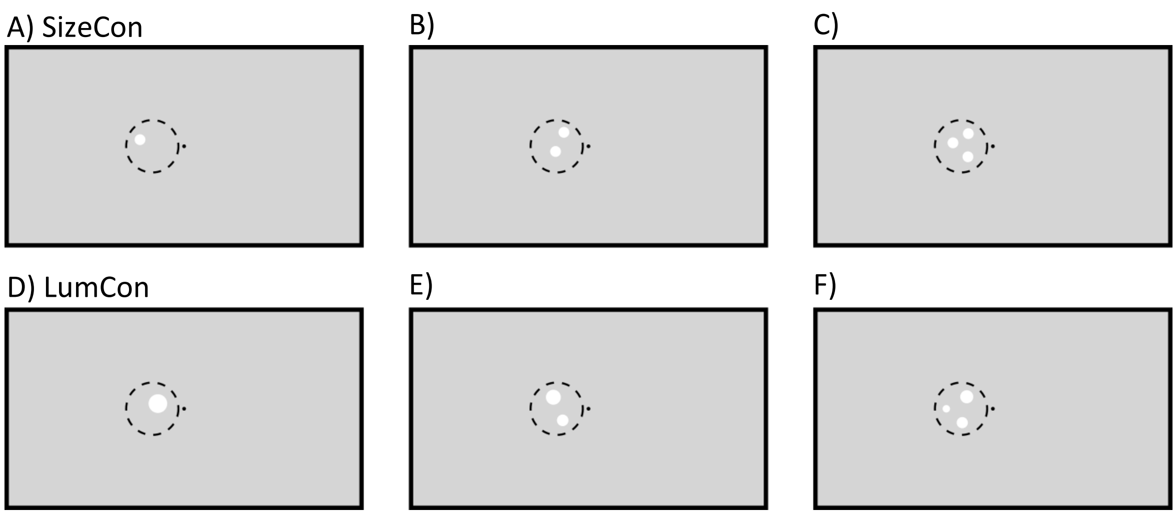


Figure 3-9: Comparison of presented stimuli (not drawn to scale). A black point (luminance: 0.2 cd/m²) in the middle of the screen on a grey (luminance: 8.6 cd/m²) background served as fixation target. Stimuli were white circular patches (luminance: 62 cd/m²) drawn in left or right (not shown here) part of the visual hemifield on vertical meridian (eye level). The one (A and D), two (B and E) and three (C and F) circular patches were pseudorandomly placed within an imaginary circle with radius 3.3° and bound to some other constrains (see text). Circular patch size was either constant (condition SizeCon: A-C) or varied by keeping the total stimulus area (and hence luminance) constant (condition LumCon: D-F).

3.3° and centre position 3.9° to the left or to the right of the fixation point, which was presented on the vertical meridian at eye level. In condition SizeCon all circular patches had a radius of 0.65°. In the condition LumCon the absolute area of the presented circular-patches was set to 8000 pixels ± 2% (uniformly distributed jitter). The radiuses were chosen pseudorandomly in a manner, that no radius would differ more than ± 40% from the mean radius and that no radius would be smaller than 0.22°. Distance between points was at least 0.39°.

3.6.2.4 Procedure

A sequence of stimuli, consisting of white circular patches was presented, one stimulus in each trial. Trials were combined to blocks with one block consisting of 30 trials. In a trial the stimulus was presented 200 ms after trial onset and lasted between 400 ms and 500 ms. The trial ended after a random time between 400 ms and 700 ms after stimulus offset (see Figure 3-10 for a schema of stimulus presentation). Jitters in stimulus duration and inter stimulus interval were pseudorandomly chosen values from a uniform distribution. In each block one standard-amount of patches (one, two or three) was presented in 24 trials (80%) while the remaining two amounts (e.g. if one was standard, two and three were deviant) were presented in three trials (10%) each, resulting in an oddball-ratio of 1 : 4. Note that due to this procedure each standard stimulus served as deviant stimulus in the two other conditions. Constraints were that the first four trials in a block were always standard trials and a deviant trial was followed by a standard trial in any case. Within a given block of trials the position (left and right part of the visual field) and the conserved feature (SizeCon or LumCon) always stayed the same. One experimental set consisted of 24 blocks, each condition (*standard value* (3) x *position* (2) x *conserved feature* (2)) was presented twice. Hence, in one set 720 trials were performed. The order of blocks was pseudorandomly distributed within a set. Between blocks an Eyelink drift correction was performed to recalibrate the Eyelink, but also to provide a breather to my subjects. Participants decided when to start the next block of trials. Every participant performed a total of 18 sets on three different days (not necessarily subsequent). Data from one subject were collected on four days due to hardware problems of the experimental setup.

In trials with a task-condition (72 trials = 10%) the fixation point became larger for 200 ms at a pseudorandomly chose point in time between 100 ms after beginning of the trial and 150 ms before the end of the trial (uniformly distributed). Responses made between 300 ms and 800 ms after task onset were considered as correct. The experiment was designed in a manner that task-conditions appeared solely in standard trials. Participants were instructed to fixate the fixation point and press a key (key down on a standard-keyboard) as fast as possible, whenever the fixation point was increased. Furthermore, subjects were told to ignore the flashed stimuli and try to reduce blinks during a block of trials.

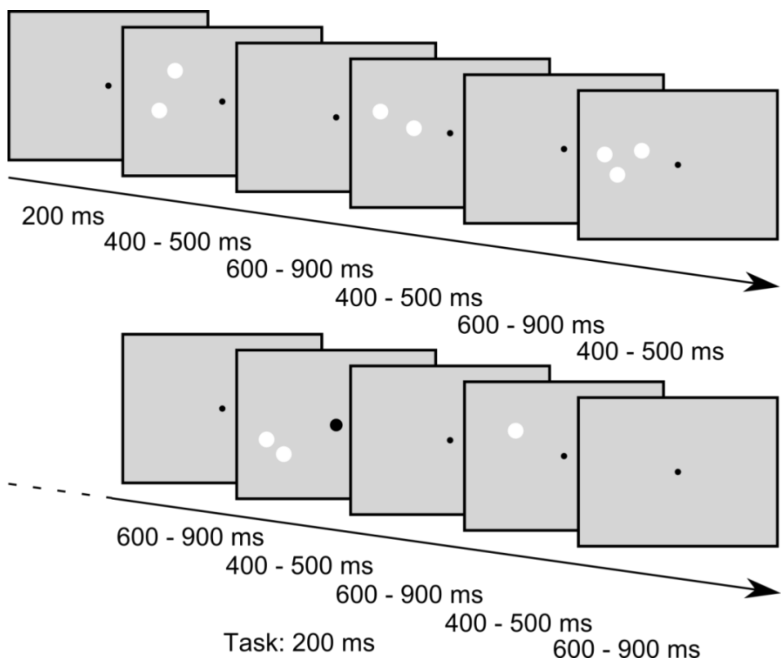


Figure 3-10: Schema of stimulus presentation. Stimuli were presented for 400 ms to 500 ms. Inter stimulus intervals lasted between 600 ms and 900 ms. In task-condition trials the fixation point's size was increased for 200 ms. For applied restrictions to stimulus order see text.

3.6.2.5 Analyses

The participants behaviour in the task, which was indicating by button presses the increase of the fixation point, was evaluated by determining the percentage of correctly pressed keys compared to all task-condition trials. Furthermore, the false alarms, button presses outside 300 ms to 800 ms after task onset, were detected.

The EEG data was further evaluated offline using Brain Vision Analyzer, MATLAB and R. In a first step the mean value of the mastoids (TP9 and TP10) was chosen as new references. Then a bandpass filter (between 0.5 Hz and 40 Hz) was applied, to reduce noise (such as influences of 50 Hz mains frequency) in unimportant frequencies and the continuous data were sliced into individual trials, starting 200 ms before stimulus onset and ending 500 ms after stimulus onset. Trials with button presses (correct and incorrect) were removed from further analysis, as were trials in which a button press would have been required, but was not performed. The mean signal amplitude of each trial in the time –110 ms up to 0 ms before stimulus onset was subtracted from the entire signal of the trial, separately for each electrode (baseline correction). In a global automatic artefact rejection all trials in which the signal of any electrode exceeded a difference of ± 100 µV within an interval of 100 ms were excluded from further analysis. In a last step trials with eye movement artefacts, such as blinking or breaking fixation, were automatically removed. Precise timing of stimulus presentation was controlled by a photo-diode attached to the screen.

Analysis was performed with two different methods. I performed a "classical" MMN analysis based on *event-related potentials* (ERPs) on the one hand and a *time-frequency-analysis* (TFA) on the other hand. Trial selection and trial averaging did not differ between both analyses and are described below. Before this, data for TFA had to be prepared. Therefore, each trial was first baseline-corrected for the time interval –200 ms to –100 ms. Then each trial was transformed with a continuous complex Morlet-wavelet-transformation (three Morlet parameters) for frequency range 1 Hz to 40 Hz (which was within the before applied filter range) with 40 logarithmic steps and for full time range (-200 ms to 500 ms). Additionally uniform scale power (unit energy normalization) wavelet normalization was applied. Due to this procedure a 40 x 700 array (hereafter named TFA-array) of positive spectral amplitude values [µV] for each trial was computed.

Trials (ERPs as well as TFA-arrays) were sorted by conditions (*presentation side* x *conserved feature* x *number* x *deviance*) and averaged within a given participant and condition separately for ERP-analysis and TFA. Pre-analysis, as descried above, might have led to variations in the amount of remaining trials between participants or conditions. The averaging within given participants and conditions ensured that potential variations in performance (blinks, breaks of fixation, button presses and bad electrode signals) did not result in an overestimation of certain conditions. Hence, each participant and each condition contributed to the results to the same degree. Since visual MMN (see Kimura, 2012 for a review) and visual ERP-effects on numbers (Plodowski et al., 2003; Libertus et al., 2007; Hyde & Spelke, 2009; Hyde & Wood, 2011) were expected to occur contralateral in parietal electrodes I averaged trials from electrodes P6, P8 and PO8 for conditions *Left* and P5, P7 and PO7 for conditions *Right*.

Significance tests on ERPs were performed following Guthrie and Buchwald (1991). This method allows conclusions based on the amount of consecutive significant samples, without the need of additional correction for multiple comparisons. To this end I first reduced the sample rate from 1000 Hz to 200 Hz by averaging over five consecutive samples. Further analysis was performed for each "resampled sample" within a time interval of 120 ms to 240 ms after stimulus onset. Hence, each test interval consisted of 24 samples. Single-sided t-tests across the participants were performed on ERP-differences (deviant condition – standard condition) averaged within the participants. This was done separately for each presentation side (Left / Right) and conserved feature (SizeCon / LumCon) and tested whether the difference in a sample was statistically significant (unequal to and below zero). This procedure resulted in 24 p-values in each condition, one for each tested sample. In addition, the first order autocorrelation (Φ) of the difference of the signals (deviant – standard) was computed in the tested time interval (120 ms to 240 ms) and averaged across participants, separately for each condition. Depending on this autocorrelation and given my experimental setting ($N = 10$ subjects; $T = 24$ samples; $p = .05$) a threshold (amount of necessary significant consecutive samples) is defined (see Guthrie & Buchwald, 1991, table 1) that had to be reached for a significant effect. For an autocorrelation $\Phi = 0.7$ this threshold was four consecutive significant samples and six consecutive significant samples for autocorrelation $\Phi = 0.9$. In a last step all consecutive significant samples that exceeded the threshold were considered as a statistically significant effect.

As an additional way to test for significance differences between standard and deviant ERPs, the ERP-amplitudes were binned within the time interval of 120 ms to 240 ms in 20 ms long bins by averaging all samples within the time bin. This procedure was repeated separately for each condition and participant. Then a single-sided t-test was performed separately for each bin, testing whether the difference between mean deviant amplitude and mean standard amplitude was below zero. All resultant p-values were corrected for multiple testing using false discovery rate (FDR) correction (Benjamini & Hochberg, 1995).

For comparisons between several conditions I performed a repeated measures *analysis of variance* (ANOVA) with ERP-amplitude values averaged in the time interval of 160 ms to 200 ms, the time interval in which the MMN was found in the first analyses. I used a three-way repeated measures ANOVA with *conserved feature* (SizeCon / LumCon), *presentation side* (Left / Right) and *deviance* (standard / deviant) as factors.

It is known that deviant stimuli elicit a stronger post stimulus response in the *theta band* (4 Hz to 8 Hz) than standard stimuli do (Herrmann et al., 2014). Hence, a positive difference (deviant – standard) in the theta band would prove the existence of MMN. In order to test this hypothesis, I averaged the responses within the time window 0 ms to 250 ms after stimulus onset and within the theta band separately for deviant and standard condition for each participant and condition. Finally I performed a single-sided t-test on whether the response in (TFA) in deviant condition was higher than in standard condition over participants.

3.6.3 Results

Data were obtained from ten participants, performing a total amount of 64,800 trials in each condition of conserved feature (SizeCon and LumCon). A total of 26.6% (n = 34,482) of the trials had to be rejected from further analysis either due to the task, button presses or artefact rejection (see chapter 3.6.2.5 Analyses). This procedure left 47,536 trials (22.0% of them deviant trials) in condition SizeCon and 47,582 trials (21.9% of them deviant trials) in condition LumCon. On average each participant performed 2,378 valid trials (std: 313) per condition (SizeCon and LumCon / Left and Right). Task performance of all participants was high: on average 89.9% of the fixation point changes were detected (std: 6.6%) within the time interval of 300 ms to 800 ms after task onset. False positive reports occurred solely in 0.4% (std: 0.3%) of all trials.

3.6.3.1 Spatial Distribution of ERPs

In a first step I analysed the spatial distribution of the ERPs. The resulting data are shown in Figure 3-11, separately for conserved feature as well as stimulus presentation side. In the data analysis, I binned mean ERPs in 50 ms bins in the time interval between 50 ms and 350 ms. The N2-component occurred mainly in the interval from 100 ms to 150 ms contralateral to the visual hemifield the stimulus was presented in.

In a next step I calculated the spatial distribution of the ERP-difference between deviant and standard condition, again separately for conserved feature as well as stimulus presentation side (see Figure 3-12). Mean ERP-differences were binned in 50 ms time intervals between 50 ms and 350 ms. One can see that the MMN occurred mainly in the time interval from 150 ms to 200 ms on the selected electrodes. MMN occurred contralateral to the stimulus presentation side.

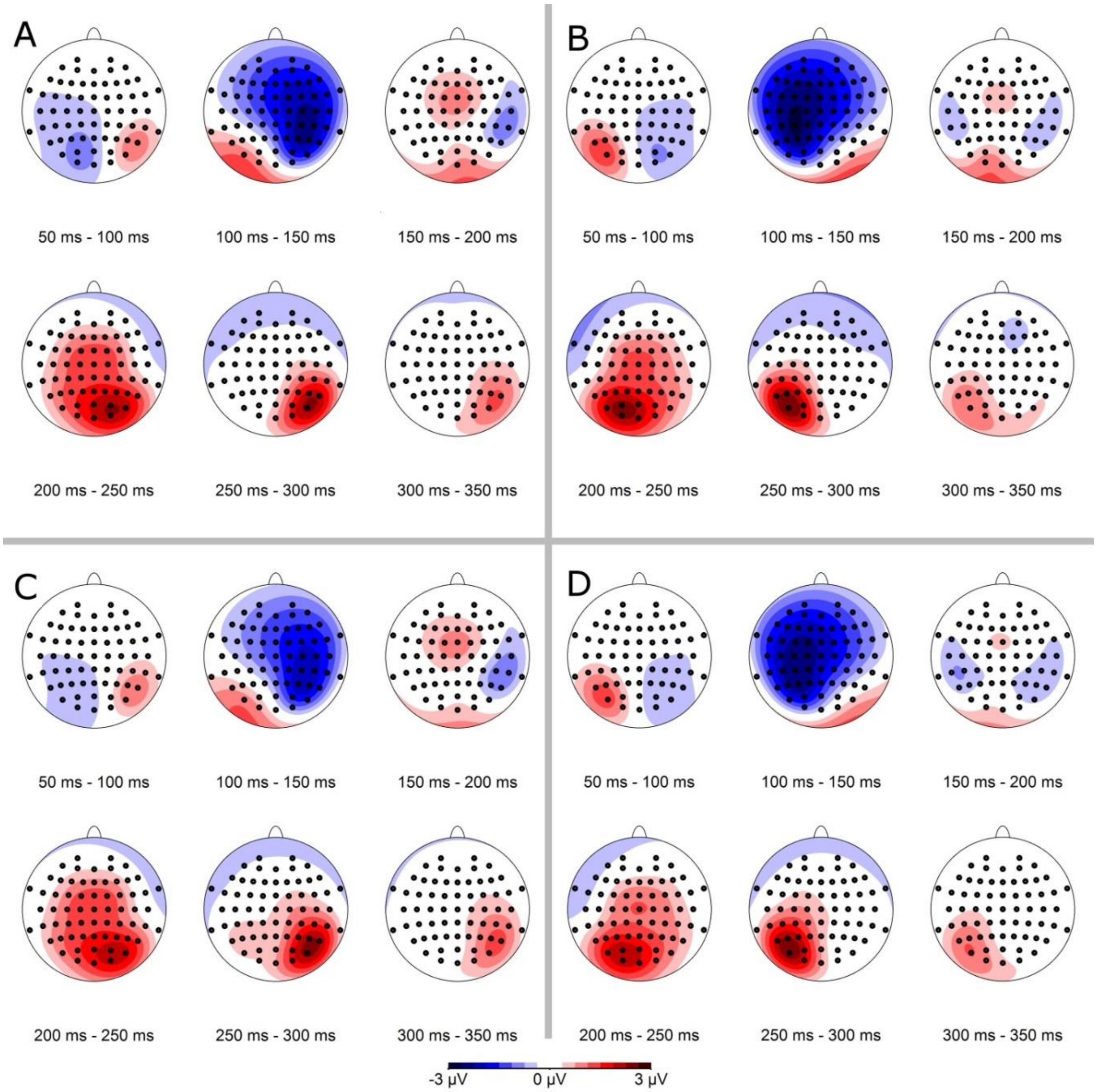


Figure 3-11: Spatial distribution of ERP-signals, separated for conserved feature (LumCon: A and B; SizeCon: C and D) and stimulus presentation position (Left: A and C; Right: B and D). ERPs were binned in 50 ms time intervals from 50 ms to 350 ms. Scale is from –3 µV (blue) to 3 µV (red). The N2-component occurs in the time interval from 100 ms to 150 ms in contralateral parieto-frontal area in all four conditions. In addition a positive component (P2) occurs ipsilateral in the parietal area in the time interval from 200 ms to 300 ms.

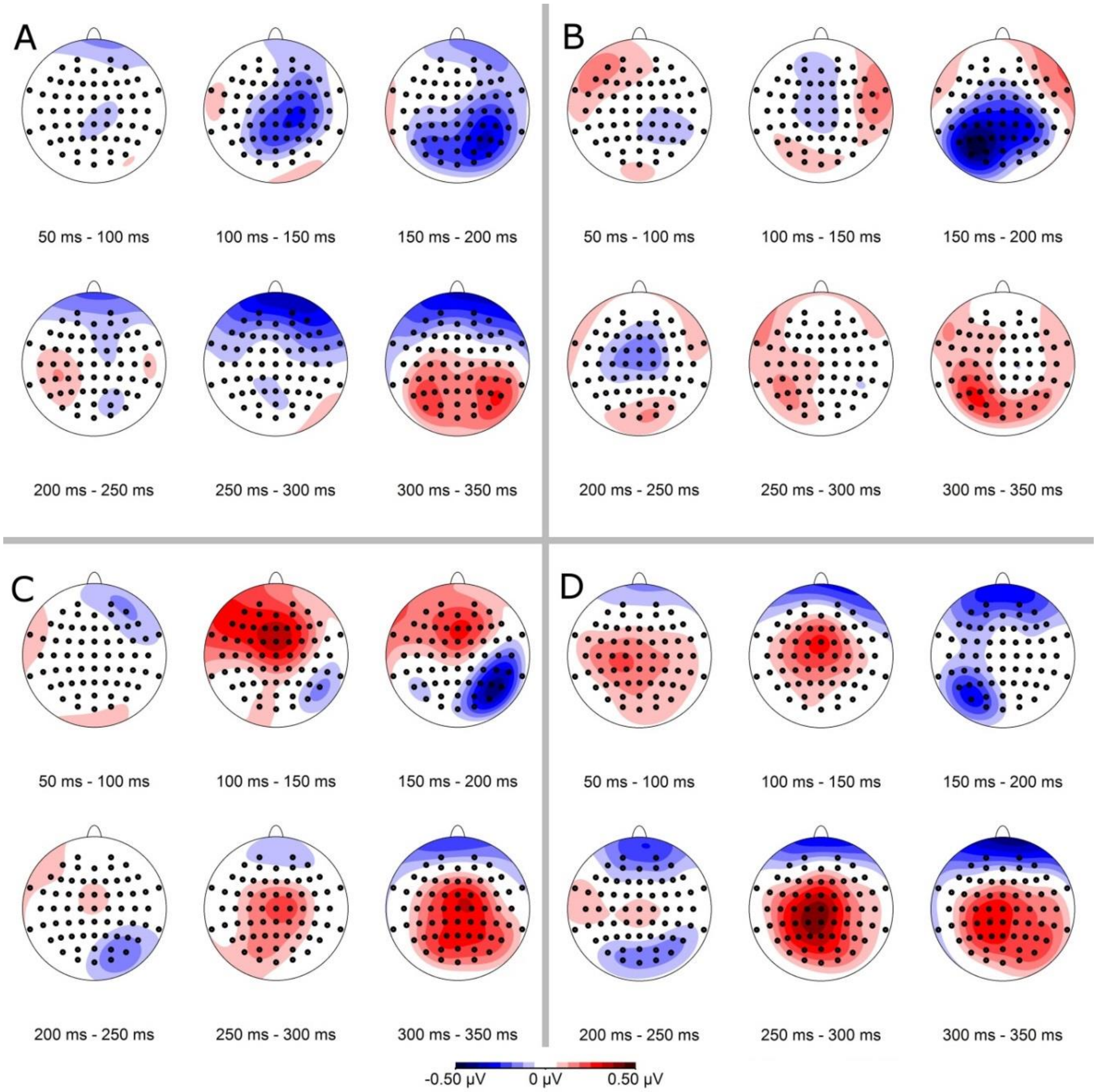


Figure 3-12: Spatial distribution of ERP-differences (condition deviant – condition standard), separated for conserved feature (LumCon: A and B; SizeCon: C and D) and stimulus presentation position (Left: A and C; Right: B and D). ERPs were binned and averaged in 50 ms time intervals from 50 ms to 350 ms. Scale is from –0.5 µV (blue) to 0.5 µV (red). The MMN in the time interval from 150 ms to 200 ms occurred in the contralateral parietal area for all four conditions.

3.6.3.2 Time Resolution of ERPs

The spatial distribution of the ERPs showed that the main effect of MMN occurred on the contralateral parietal electrodes. Hence, it was appropriate to concentrate my further analysis with higher time resolution than in the last chapter, on the electrodes P6, P8 and PO8 for condition Left and P5, P7 and PO7 for condition Right. Therefore, as a next step, I compared the time resolution of the ERPs, averaged over these electrodes. Since the ERP amplitudes were first averaged within and then across numbers, each number had an

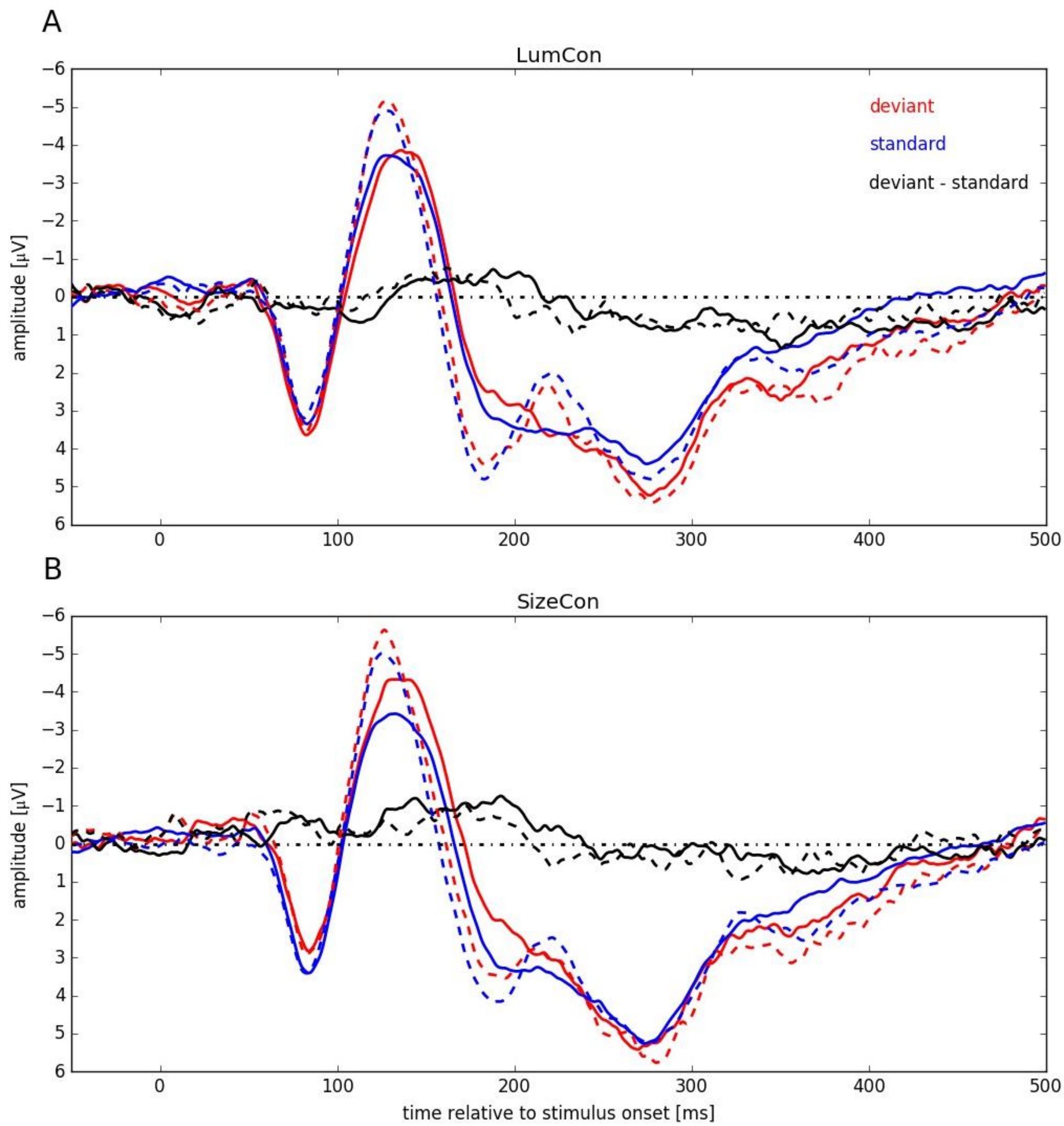


Figure 3-13: ERP signals from a typical single subject (subject VI) for both conserved features (LumCon: A; SizeCon: B). ERPs are shown in red (deviant condition) and blue (standard condition). Difference between ERPs (deviant condition – standard condition) is shown in black. ERPs from conditions with stimulus presentation side Left (averaged over electrodes P6, P8 and PO8) are shown in continuous lines (dashed lines for Right, averaged over electrodes P5, P7 and PO7). Amplitudes [µV] are plotted over time relative to stimulus onset [ms].

equal contribution to the results. As described above, each deviant stimulus served also as standard stimulus in another condition, so that deviant and standard stimulus differed only by presentation rate. Single subject data showed clear P1- (between 75 ms and 90 ms) and N2-components (between 130 ms and 150 ms). A typical dataset from a single subject (from subject VI) is shown in Figure 3-13. Specifically, the N2-compontens in the deviant conditions peaked higher and lasted longer than N2-components in the standard conditions. Hence, the difference between ERP-signals (ERP deviant – ERP standard) was negative in the time window from 130 ms up to 220 ms.

In a next step I pooled the ERPs across subjects within the four conditions (*LumCon* x *SizeCon*) and (*Left* x *Right*) (see Figure 3-14). Pooled data showed results very similar to the single subject data. For both conserved features a P1-component in the time interval from 50 ms up to 105 ms with a peak at about 80 ms and a N2-component in the time interval from 105 ms up to 180 ms with a peak at about 145 ms was present. Again the N2 component in deviant conditions peaked higher and lasted longer than in standard conditions resulting in a negative difference (ERP deviant – ERP standard) between 130 ms and 215 ms (MMN). Furthermore, the P2-components (180 ms to 400 ms with a peak at around 280 ms) differed between deviant and standard condition. The deviant condition was more positive resulting in a positive difference for times above 310 ms for all four conditions.

I tested for significant differences between deviant and standard ERPs by applying the method introduced by Guthrie and Buchwald (1991). To this end, I calculated single-sided t-tests, separately for stimulus presentation positions and conserved feature, thereby testing the hypothesis that the difference between amplitudes in deviant and in standard conditions was below zero (see chapter 3.6.2.5 Analyses). The analysis revealed for condition LumCon for both presentation sides eleven significant continuous samples between 150 ms and 220 ms. For condition SizeCon Left 18 continuous samples between 125 ms and 214 ms and for SizeCon Right seven continuous samples between 160 ms and 194 ms were statistically significant. First order autocorrelation of ERP differences in the investigated time interval (120 ms to 240 ms) was $\Phi = 0.84$ (Left) and $\Phi = 0.91$ (Right) for

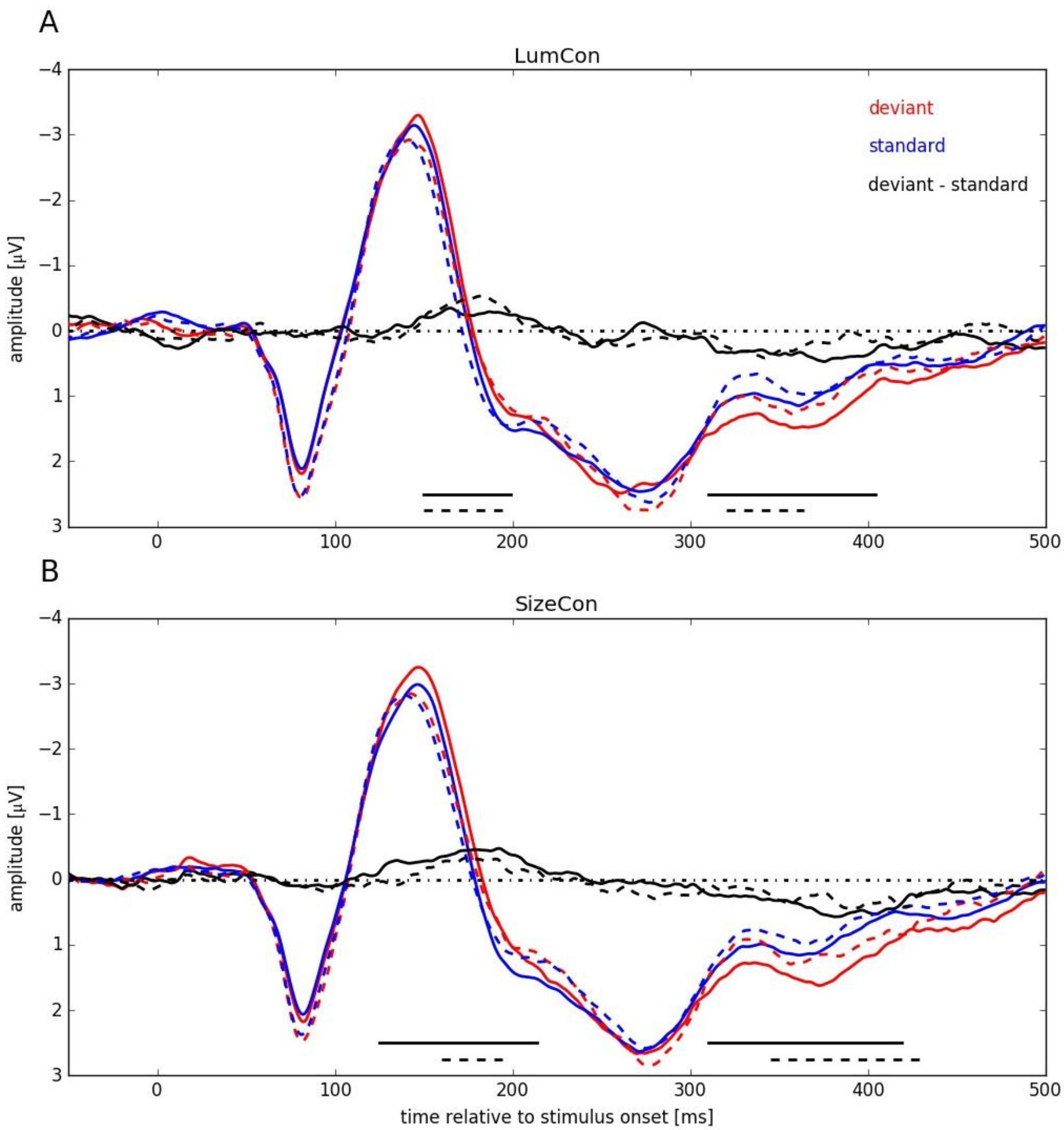


Figure 3-14: ERP signals pooled over all participants for both conserved features (LumCon: A; SizeCon: B). ERPs are shown in red (deviant condition) and blue (standard condition). Difference between ERPs (deviant condition – standard condition) is shown in black. ERPs from conditions with stimulus presentation side Left (averaged over electrodes P6, P8 and PO8) are shown in continuous lines (dashed lines for Right, averaged over electrodes P5, P7 and PO7). Amplitudes [µV] are plotted over time relative to stimulus onset [ms]. Black lines at the bottom indicate significant differences between deviant and standard condition.

condition LumCon and Φ = 0.82 (Left) and Φ = 0.86 (Right) for condition SizeCon. According to Guthrie and Buchwald (1991, table 1), given the settings in my experiment (N = 10 subjects; T = 24 samples; p = .05) and the results of my analysis, six continuous significant samples would indicate a significant difference between deviant and standard ERPs. Hence, the MMN as found in all four conditions was statistically significant. An additional analysis with data binned in 20 ms intervals, individually tested and then corrected for multiple comparisons (FDR-correction, Benjamini & Hochberg, 1995) yielded similar results. In particular these results showed significant intervals between 160 ms and 180 ms in all four conditions (all $t(0.95; 9) > 2.73$, $p < .043$). The interval 180 ms to 200 ms was significant in SizeCon Left and LumCon Right (all $t(0.95; 9) > 3.85$, $p < .016$) and showed a trend for the remaining two conditions $t(0.95; 9) > 2.21$, $p < .073$).

In order to compare the mean ERPs within these intervals (161 ms to 200 ms) I performed a three-way repeated measures ANOVA with *presentation side* (Left / Right), *conserved feature* (LumCon / SizeCon) and *deviance* (standard / deviant) as factors. I found two main effects for *deviance* ($F(1,9) = 36.71$, $p < .001$) and for *conserved feature* ($F(1,9) = 24.28$, $p < .001$). The other main effect and all interactions were not significant (all $F < 3.28$, $p > .1$). The main effect for *conserved feature* indicated that in the chosen interval the mean amplitude in condition LumCon was higher (mean(LumCon amplitude) = 0.17 µV) than the mean amplitude in condition SizeCon (mean(SizeCon amplitude) = –0.20 µV). The main effect on *deviance* reflected the global MMN (mean(deviant amplitude) = –0.19 µV; mean(standard amplitude) = 0.16 µV) within the chosen interval. Since all interactions with *deviance* were not significant, no significant differences in MMN could be found for *presentation side*, *conserved feature* or the combination of both parameters together. Note that due to the chosen electrodes (Left: P6, P8, PO8; Right: P5, P7, PO7) the key effect of visual hemifield (as presented in Figure 3-12) was removed. Hence, in the ANOVA the finding of “no main effect of presentation side” reflected that there was no significant lateralization of MMN exceeding the anatomically lateralization of presentation in different visual hemifields.

Beyond the main hypothesis of my study concerning the MMN, it was noticeable that the ERPs showed differences in the late P300 component (300 ms to 450 ms) in a way that deviant responses had a higher amplitude than standard responses (see Figure 3-14). Therefore, I tested the difference in this time range with the method introduced by

Guthrie and Buchwald (1991), as described before with the modification that, since I had no previous expectations of this difference, a two-sided t-test was used instead of the single-sided t-test used for MMN-analysis. First order autocorrelation (Φ) of all four conditions lay between $0.79 < \Phi < 0.86$. The test-interval contained 30 samples so that, according to Guthrie and Buchwald (1991, table 1), nine significant samples would at least be expected for a significant effect. In all four conditions between nine and 22 significant consecutive samples were found, resulting in significant effects for LumCon Left (310 ms to 404 ms), LumCon Right (320 ms to 364 ms), SizeCon Left (310 ms to 419 ms) and SizeCon Right (345 ms to 429 ms).

3.6.3.3 Time-Frequency-Analysis

In addition to the classical analysis of ERPs I also performed a *time-frequency-analysis* (TFA) using complex Morlet-wavelet-transformations for each trial. Due to this procedure the positive and negative signals of each ERP were transformed into purely positive spectral amplitudes in time and frequency. As a consequence of this transformation, in the adjacent averaging no components could "cancel out", as this is the case for non-stimulus-locked events in ERP analysis (see chapter 2.3.5 Time-Frequency-Analysis (TFA)). Hence, this analysis showed not only evoked but also induced responses (c.f. Herrmann et al., 2014). The spectral amplitudes for both presentation sides (Left and Right) and both conserved features (LumCon and SizeCon) for deviant and standard condition as well as the difference (Deviant – Standard) are shown in Figure 3-15. All conditions (deviant as well as standard) showed a broad activity in the *delta band* (1 Hz to 4 Hz) after stimulus onset. The much weaker post-stimulus activity in the higher frequency ranges (4 Hz to 12 Hz) lasted shorter and differed between deviant and standard condition. A clear positivity became apparent in difference plots (Figure 3-15 C, F, I and L), which is indicative of a stronger response to deviant in contrast to standard stimuli, in the lower frequencies (2 Hz to 8 Hz) in the time after stimulus onset (0 ms to 250 ms). A single-sided t-test on averaged values in this time (0 ms to 250 ms) and frequency (4 Hz to 8 Hz) range showed a significant stronger activity as response to the deviant stimulus for condition LumCon Right ($t(0.95; 9) = 2.25$; $p = .026$) and SizeCon Left ($t(0.95; 9) = 2.66$; $p = .013$). The other

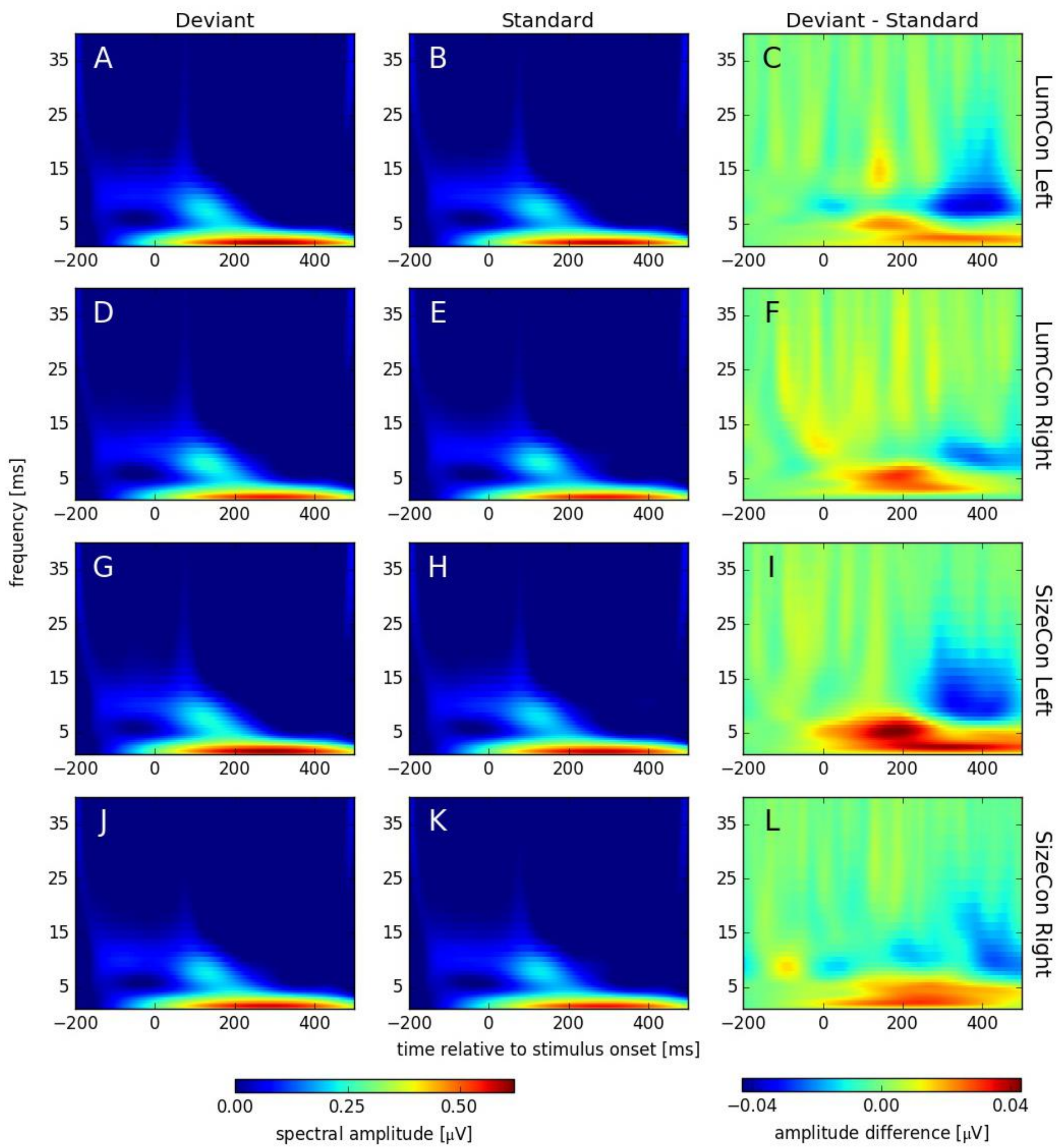


Figure 3-15: Spectral amplitudes [µV] of continuous complex wavelet transformation (time-frequency-analysis) plotted for time [ms] at the abscissa and frequency [Hz] at the ordinate. The first column (A, D, G and J) shows responses to deviant and the second column (B, E, H and K) responses to standard stimuli. The third column (C, F, I and L) displays the difference (deviant – standard) of both spectral amplitudes. The rows correspond to the presentation conditions: LumCon Left (A-C), LumCon Right (D-F), SizeCon Left (G-I) and SizeCon Right (J-L).

two conditions revealed no significant differences in this time-frequency-interval (all ($t(0.95; 9) < 1.2$; $p > 0.14$)). Furthermore, a negativity, i.e. stronger responses to standard stimuli compared to deviant stimuli, occurred in the time range above 350 ms in the *alpha band* (8 Hz up to 17 Hz) in all four conditions.

3.6.4 Discussion

I performed a classical visual mismatch negativity experiment on numerosity. Across conditions, displays with different numbers of circular patches (1, 2 or 3) served as standard and as deviant stimulus, so that standard and deviant stimuli differed solely in presentation frequency. Participants were engaged in a difficult perceptual task close to the fixation point drawing attention away from the lateralized presented stimuli. Low-level stimulus features (patch size and absolute luminance) were separately varied in distinct conditions. I could unequivocally show lateralized visual mismatch negativity for both conditions, LumCon and SizeCon, respectively.

The instantaneous perception of small numerical magnitudes, called subitizing, has often been assumed to be pre-attentive (e.g. Trick & Pylyshyn, 1994). More recent studies showed that subitizing, in contrast to number perception of larger magnitudes (probably processed by the *approximate number system* (ANS)), was influenced by attentional load. These studies documented an influence on subitizing by closely preceding letter identification tasks (attentional blink paradigm) (Olivers & Watson, 2008) and inattentional blindness paradigms (Railo et al., 2008). These findings were considered evidence that subitizing is not pre-attentive (Anobile et al., 2012). The number of patches as employed in my MMN study were well in the subitizing range. Accordingly, the findings by Anobile and colleagues would have suggested to not find a MMN in my study. Different from this prediction but according to my hypothesis I found a visual MMN as response to numerosity changes, both in the pure event-related potentials (ERPs) as well as in a time-frequency-analysis (TFA). In ERP analysis this effect was significant for all four conditions within the time interval of 125 ms to 220 ms. TFA yielded similar results. In this analysis two out of four conditions, LumCon Right and SizeCon Left, showed a significant positive difference between responses on deviant and standard stimuli in the *theta band* (4 Hz to 8 Hz). In the two remaining conditions the graphs showed the same pattern for differences but significance was not reached. According to the relatively small amplitude of MMN in my data, the relatively small cohort of participants and the fact that TFA extends one-dimensional data into two dimensions, this must not be seen as a disprove of MMN in these conditions. Previous findings (Ruusuvirta & Astikainen, 2016) with auditory stimuli reported MMN on ratio changes. They presented six auditory stimuli sequentially consisting of two types of stimuli, differing in frequency (for simplicity named A and B). As standard stimuli served six tones with a ratio of 3 : 3 (three tones with frequency A and three tones with frequency B). Deviant stimuli consisted of six tones that had a ratio of 2 : 4 (e.g. two stimuli with frequency A and four stimuli with frequency B) or 1 : 5. Ruusuvirta and Astikainen reported MMN solely for large ratio changes from 3 : 3 to 1 : 5 but not for smaller ratio changes (from 3 : 3 to 2 : 4). With my experimental setting I could show visual MMN for amount changes of 1 to 3, which is comparable to the reported larger ratio changes (3 : 3 to 1 : 5) in the auditory experiment.

Participants in my experiment were not instructed to attend to the presented magnitude or report the perceived number. Hence, discrimination between ANS and OTS in my experiment is hardly accomplishable. Therefore, the observed *mismatch negativity* (MMN) might reflect pre-attentiveness of the ANS or of the OTS. However, my experiment provided evidence that numbers in this low (subitizing) range are processed pre-attentively, no matter by which of the two systems.

The influence of number presentation on the N2 component has been investigated before. Hyde and Spelke (2009) examined magnitudes of dot patterns with a small number range (numbers 1, 2 and 3) and a large number range (numbers 8, 16 and 24) without any task. They found that N2 components (140 ms to 175 ms) for small numbers became more negative with increasing number magnitude, while for large numbers the opposite was true. Decreasing N2 amplitude with increasing number of dots has also been shown for the values 1 to 4 and 6 to 9 (Libertus et al., 2007). Here participants had to judge actively whether the presented number was smaller or larger than number 5. Decrement became saturated for numbers above 5. This effect was replicated for higher numbers (12, 18 and 24) (Gebuis & Reynvoet, 2012). The differences in N2 components disappeared when participants were engaged in a high attentional load task (Hyde & Wood, 2011).

However, the reported effect of a decreasing N2 component with increasing number of presented stimuli cannot account for the MMN I found in my study. Reason for this is that in my experiment deviant and standard stimuli consisted of all three dot amounts and differed only in presentation rate. Any effect caused by cardinality of the stimuli should hence cancel out in the average over all three stimuli and remaining differences must be visual MMNs.

Although this was not the main purpose of my study, I found a significant stronger response to standard stimuli compared to deviant stimuli in the late P300 component in the time range of 310 ms up to 429 ms in each condition. This pattern was also found in the TFA where standard stimuli elicited stronger spectral amplitudes than deviant stimuli in the *alpha band* (8 Hz to 17 Hz) in a time range beyond 350 ms post stimulus onset. Up to date the neurophysiological basis of the P300 component is not well understood. Some experimental evidence suggested an interaction of frontal lobe and temporal-parietal areas to be involved in generating the P300 (see Huang et al., 2015 for a review). Furthermore, it was hypothesized that in oddball paradigms P300 components could be elicited as response to detection of rare stimuli and might be linked to working memory (e.g. McCarthy et al., 1997). Hence, the differences in P300 might be an indication that the change in numerosity was processed by the participants, although they were engaged in a difficult task. However, this finding does not affect the statement that number processing in the subitizing range was pre-attentive, since the effects of MMN occurred well before the effects in the P300 component.

Since the presentation of the stimuli was lateralized (stimuli were located only in the left or the right half of the visual field), I expected the strongest MMN responses contralateral on parietal electrodes (c.f. Plodowski et al., 2003; Libertus et al., 2007; Hyde & Spelke, 2009; Hyde & Wood, 2011). My data were in line with this hypothesis (see Figure 3-12). FMRI studies reported a parietal activation for number processing (for example number comparison) in the right as well as in the left hemisphere (Chochon et al., 1999; Pinel et al., 2001). The functional locus of visual MMN is supposed to be in the right occipital visual extrastriate area (Kimura, 2012). The repeated measures ANOVA of my data showed no significant interactions of presentation side and MMN. It is important to note that the effect of stimulus presentation in different visual hemifields (see Figure 3-12) was removed in data processed in this ANOVA due to the selection of different electrodes for different presentation side (see chapter 3.6.2.5 Analyses). Hence, the results of the ANOVA that revealed "no main effect on response side" actually means, that there is no effect on visual MMN on response side exceeding the beforehand assumed lateralization of response side.

A critical point in all numerosity experiments is to distinguish between effects of low-level-features and "real" numerosity (e.g. Burr & Ross, 2008). Importantly, it is impossible to correct for all low-level-features at the same time. For example, increasing the number of circular patches while keeping the radius of the patches constant leads to an increase in overall luminance. On the other hand, keeping luminance constant requires an appropriate adjustment (i.e. change) of patch size (more patches are on average smaller) or patch luminance (more patches are less luminant). To cope with this problem, I used two different conditions. In one condition luminance was held constant (LumCon) by decreasing patch size with increasing number of patches. In the second condition, patch size was held constant by increasing luminance with increasing number of patches. Hence, it might be the case that in my experiment in one condition the change in luminance and in the other condition the change in patch size elicited visual MMN. A hint that this might not be the case is that the spatial distribution in both conditions was very similar. In addition, in other studies investigating the effects of stimulus size (e.g. Kimura et al., 2008a) and luminance (e.g. Kimura et al., 2008b) the visual MMN was found at the electrodes PO7 and PO8 in a later time range (240 ms to 260 ms) than at the same electrodes in my study (150 ms to 200 ms). Hence, I consider it as unlikely that the measured visual MMN in my experiment was a consequence of patch size or luminance changes. Other possible low-level-features that might affect my findings are *total circumference* and *density* of the patches. The impact of the latter feature has been investigated for a larger number of dots (e.g. Gebuis & Reynvoet, 2012). But as I presented only up to three patches, it was impossible to correct for patch density. Still a potential influence of total circumference, which means that the reported MMN might have arisen from this stimulus feature instead of numerosity, cannot be ruled out. However, to the best of my knowledge visual MMN has not yet been demonstrated for total circumference.

4 General Discussion and Outlook

In this thesis I used psychophysical methods and electroencephalography (EEG) to investigate the human sense of number and the (neuronal) processes underlying this sense. Of special interest was the question under which conditions the SNARC effect (*spatial numerical association of response codes*) manifests and which conclusions one can draw out of the nature of the SNARC effect concerning number representation in the *approximate number system* (ANS) in general and the form of the *mental number line* (MNL) in particular. An additional part of my research comprised the MARC effect (*linguistic markedness of response codes*), which is another essential numerical effect that allows for insights on number processing in the ANS. In addition to the ANS, I studied the *object tracking system* (OTS), which is known to be responsible for processing small number magnitudes within the subitizing range. By means of a mismatch negativity task I explored the question of whether numbers in the subitizing range are processed pre-attentively or not.

4.1 Evidences for a Distributed SNARC Network

The SNARC effect is a well-known and intensely investigated effect that is commonly seen as evidence that the human brain processes numbers on a so-called *mental number line* (MNL) (see Winter et al., 2015 for a review). This MNL is assumed to range from the left for small numbers to the right for large numbers. The SNARC effect has been shown for many different effectors, such as bimanual responses (Dehaene et al., 1993), unimanual responses (Fischer, 2003), pedal responses (Schwarz & Müller, 2006), saccadic eye movements (Schwarz & Keus, 2004), vocal responses (Leth-Steensen & Citta, 2016) and grip movements (Andres at al., 2004). Given the existence of the SNARC effect as tested with all these different effectors one could argue that the SNARC effect was effector independent. Since different effectors (eyes vs. hands vs. feet) are controlled by different brain-regions, the effector independency of the SNARC effect would have pointed towards a generation of the SNARC effect in a single, early processing stage, independent from response-preparation and response-execution stages. In this vein, some psychophysical (e.g. Keus & Schwarz, 2005) and EEG studies (Keus et al., 2005; Gevers et al., 2006b) on the

SNARC effect pointed towards an emergence of the SNARC effect in an early or mid-level response-selection stage.

In my first study, I tested the strength of the SNARC effect in three different effectors (*Finger*, *Eye* and *Arm*) and compared it within participants. As a result, I received one significant correlation between two effectors, but no significant correlation for the other two pairs of effectors. If SNARC had been indeed effector independent, significant correlations between all three effectors should have occurred. Further analyses revealed that the proportion of participants showing a significant SNARC effect in all three effectors differed significantly from the proportion that would have been expected if the SNARC effect was statistically independent from the effector. This result was obtained in pairwise comparison between the measured effectors, too. Therefore, I concluded that the strength of the SNARC effect depends on the chosen effector and, hence, is effector specific. Such effector specificity is in contrast to the assumption that the SNARC effect solely arises in the response-selection stage, since in this relatively early stage no effector-dependent effects would be assumed.

The SNARC effect has also been claimed to be amodal, i.e. to be independent of the sensory modality of the stimuli (Nuerk et al., 2005). In this study, the SNARC effect was tested with different presentation modalities (Arabic numbers, written number words, spoken number words and dice pattern) and no significant difference in the strength of the SNARC effect between the modalities was found. These findings were challenged by Wood and colleagues (2006b), who did not find significant correlations between SNARC strength resulting from auditory stimulus presentation and the SNARC strength resulting from the three visual number presentations. This was considered evidence that the SNARC effect might not be amodal. If the SNARC effect was in fact amodal, this would clearly point towards a generation of the SNARC effect in late supramodal processing stages as e.g. the parietal cortex. In my second study, I investigated the SNARC effect for four different spatial orientations: *Horizontal*, *Vertical*, *Diagonal_1:30* (left down to right up) and *Diagonal_4:30* (left up to right down). This experiment was performed with auditory and visual stimuli measured in the same subjects for all four orientations and both sensory modalities. This approach allowed me to compare the SNARC strength evoked by auditory and visual stimuli within participants. Repeated measures ANOVA revealed significant differences in SNARC strength between auditory and visual modalities indicating that the SNARC effect is not amodal. Hence, these findings suggest an involvement of those brain areas in the generation of the SNARC effect, which take part in the early task execution.

The results from my first two studies challenge those from previous studies that hypothesized a generic SNARC module which might, for example, be located in a late response-related processing stage, putative in response selection (e.g. Keus & Schwarz, 2005). Since the existence of a generic SNARC module and a distributed SNARC network are not mutually exclusive it might be reasonable to combine both approaches in order to resolve the issue of seeming contradictory findings. More specifically, I consider it likely that there is one instance in the response-related processing stage that is basically and essentially involved in the generation of the SNARC effect, but along with this stage other instances, early sensory-modality-dependent and late effector-dependent, modulate the SNARC effect, too. In other words: I propose a distributed SNARC network with multiple stages. The main stage could be a *central number stage* (CNS) being combined with *early and late processing stages* that modulate the SNARC effect (see Figure 4-1). The CNS could be located in the parietal cortex (e.g. Göbel et al., 2006), where neurons are considered late in the sensory processing but early in the motor processing (Andersen, 1995; Shulman et al., 2002). Furthermore, it is known, for example, from functional near-infrared spectroscopy, that bilaterally the *horizontal segment of the intraparietal sulcus* (hIPS) and the *left angular gyrus* (AG), both regions within the parietal lobe, are active during a SNARC task (Cutini et al., 2012). These regions are also active during other number related tasks (Chochon et al., 1999; Dehaene et al., 1999; Piazza et al., 2004; Jacob & Nieder, 2009). The *early processing stages* (EPS) might be located (among others) in the *auditory cortex* and in the *number form area* (NFA). This latter region is located in the inferior temporal gyrus and is known to be important for processing of visually perceived digits, as revealed by a recent transcranial magnetic stimulation experiment (e.g. Grotheer et al., 2016; see Merkley et al., 2016 for a review on NFA). The *late processing stages* (LPS), may be found, for instance, in the functional equivalents of monkeys' *parietal reach region* (PRR) for hand movements (see Vesia & Crawford, 2012 for a review) or in functional equivalents of monkeys' *lateral intraparietal area* (LIP) for saccades in the human brain (e.g. Konen et al., 2004, 2007; Konen & Kastner, 2008; Kleiser et al., 2009). In the area LIP, like for neighbouring *ventral intraparietal area* (VIP) in monkeys, neurons being tuned for numerical value have been identified (Roitman et al., 2007). These early and late stages would be responsible for modulations of the SNARC effect by the sensory modality and/or the effector.

This idea leads to the question of the implications of the distributed SNARC network on number perception. Given the existence of the proposed *central number stage* (CNS) and given that several studies have shown neural correlates of the processing of numerical information in the hIPS and the AG, I suggest the origin of the number processing in the CNS. The relationship between numbers and space, the *mental number line* (Dehaene et al., 1993) or alternatively the origin of the *polarity correspondence principle* (Proctor & Cho, 2006) may have their basis in this CNS. It is important to note that the CNS may consist of a single brain area or various brain areas which together generate the association between numbers and space. With my study no conclusions on the exact form of this proposed CNS can be drawn. The existence of a CNS performing the above described function, however, is plausible since abstract number perception might eventually depend on the sensory modality, but there is no conceivable reason why number perception should depend on an effector. Hence, the described differences in SNARC strength between effectors and between sensory modalities should be interpreted as "differences in SNARC strength" and not as differences in the underlying association between numbers and space.

As some effectors have more in common than others (for instance, responses given by two fingers of one hand are closer related to responses given by two fingers of two hands than to behavioural responses given by means of saccadic eye movements) it might be the case that some effectors share a common LPS. This would, for example, account for the significant correlation between effector *Finger* and effector *Arm* reported in

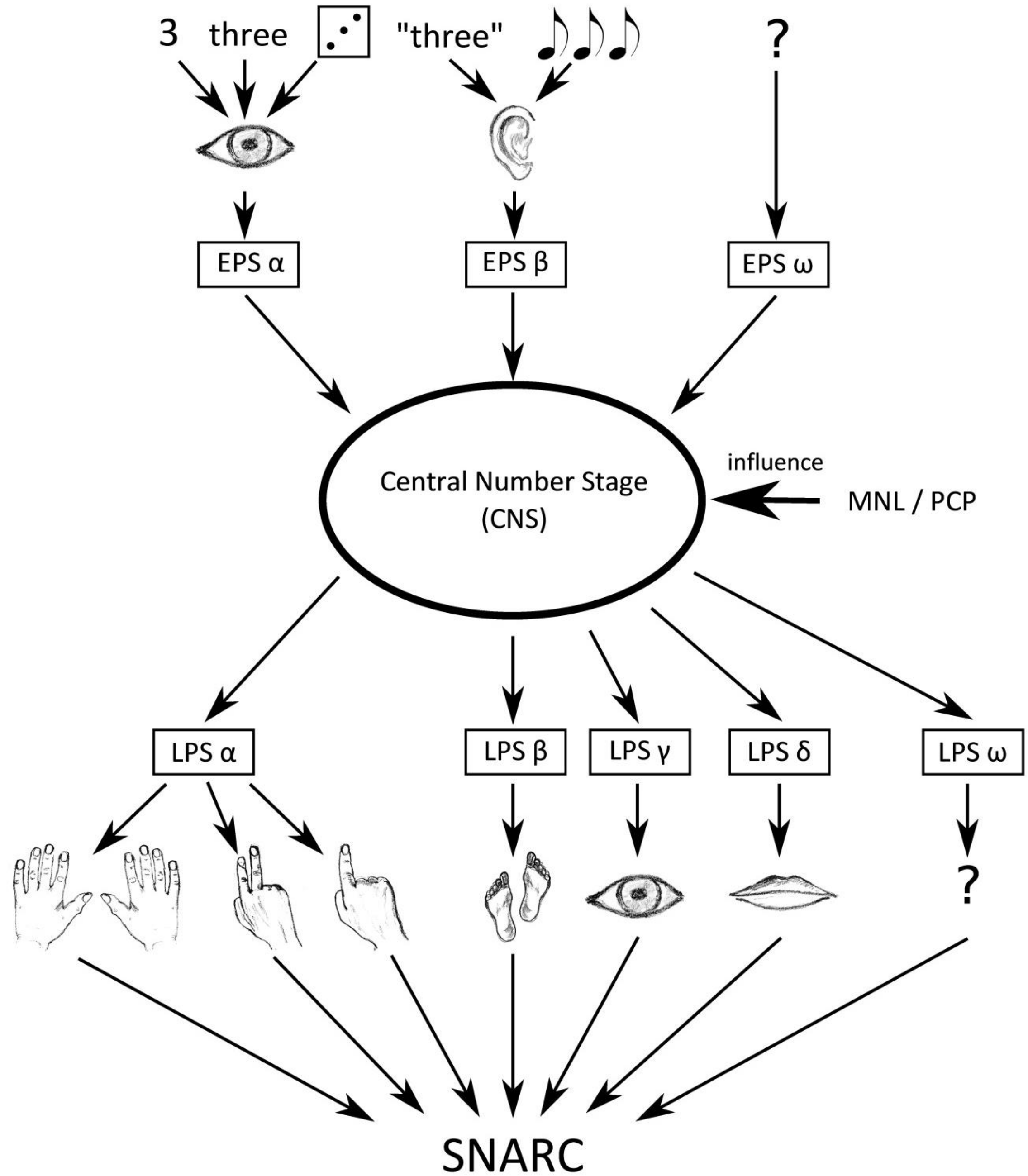


Figure 4-1: Schema of the proposed distributed SNARC network. Numbers are presented in different modalities for example as visual stimuli (Arabic digits, written number words, dice pattern, etc.) and perceived with the eyes or as auditory stimuli (spoken words, tone sequence, etc.) and perceived by the ears. This percept might be modulated by (different) *early processing stages* (EPS) and is than further processed in the *central number stage* (CNS). At this central stage any interaction between numbers and space, resultant from a *mental number line* (MNL) or due to the *polarity correspondence principle* (PCP), happens. After the CNS the selected response might be further modulated in (different) *late processing stages* (LPS) before finally indicated by one of the different effectors (bimanual responses, responses with two fingers, unimanual pointing responses, pedal responses, saccadic responses, vocal responses, etc.) resultant in the measured SNARC effect.

my first study. Hartmann and colleagues (2014) reported a vertical SNARC effect measured with bimanual responses, but no vertical SNARC effect measured with one hand and one foot. In the context of my hypothesis (provided above) this could be explained, when hand and feet were processed in different LPSs. Moreover, the significant correlations between SNARC effects investigated with visually presented Arabic digits and visually presented number words could point to a common EPS for visual perception, for example, the *number form area* (see Merkley et al., 2016 for a review on NFA).

Early and late processing stages modulate the SNARC effect. Hence, if an experiment included solely one sensory modality or just one effector, caution is necessary when interpreting the SNARC effect in terms of the relationship between numbers and space. Results from such experiments might, or might not, depend on "non-number effects" thus influencing possible conclusions on the mental number line or any other number related theory. However, in addition to the factors sensory modality and effector, other parameters might influence the SNARC effect, such as reading and writing habits (Dehaene et al., 1993), finger counting habits (Fischer, 2008) and the applied reference frame (Viarouge et al., 2014a).

4.2 No MARC Effect in Saccadic Responses

The main purpose of my thesis was the investigation of the interaction of numbers and space, as for instance revealed by the SNARC effect. In addition, my studies allowed investigating another number related effect, the MARC effect (*linguistic markedness of response codes*). Hence, the drawing of further conclusions on number processing in the ANS was possible. The MARC effect (Berch et al., 1999; Nuerk et al., 2004) describes the phenomenon that participants respond faster to even numbers on the right-hand side and to odd numbers on the left-hand side. This phenomenon has been linked to the linguistic markedness of words resulting in faster reactions when the markedness of two categories is congruent ("right" and "even" are linguistically nonmarked, while "left" and "odd" are marked).

Another possible explanation with similar but more general assumptions for the MARC effect is provided by the *polarity correspondence principle* (Proctor & Cho, 2006; Cho & Proctor, 2007), stating the decrease of response time as a consequence of matching polarities. According to this idea, “right” and “even” are [+] polar, while “left” and “odd” are [–] polar. However, the MARC effect is often reported for bimanual responses to the left and to the right (Berch et al., 1999; Nuerk et al., 2004; Cho & Proctor, 2007; Huber et al., 2015; Roettger & Domahs, 2015) and has been found to be strongest for number words (Nuerk et al., 2004). Hence, I expected to find a MARC effect in my first study and for horizontal responses in my second study. In my first study, I indeed found a MARC effect for bimanual (*Finger*) and pointing (*Arm*) responses, but I did not find a MARC effect for saccadic responses (*Eye*). In my second study, responses solely were given by means of saccadic eye movements, and horizontal responses yielded no significant MARC effect, either. Even in the auditory stimulus presentation modality, which was supposed to reveal a strong MARC effect, I did not find this effect. The missing of MARC effect for saccadic responses is very well in line with the findings of Schwarz and Keus (2004), who did not report a MARC effect in their saccadic experiments (with visual presented stimuli), although they tested (implicitly) for it.

My second study allowed testing for a MARC effect on the vertical axis and both diagonal axes. In order to do so, I had to determine the markedness of the additionally used categories (up and down). Since my participants were Germans, just like the participants from Nuerk and colleagues (2004), the markedness of the terms “left” and “odd” in contrast to the unmarked “right” and “even” was beyond dispute. Unfortunately, the markedness of the German words “up” and “down” (in German: “oben” and “unten”) is not that obvious. In contrast to “odd” and “even” there is no *phonologic* or *morphologic* markedness of these words in German. One could argue that a kind of *cognitive* markedness can be expected in a way that “up” is unmarked, while “down” is marked. Reason for this would be that the head is “up”, or that there is a downward limit (earth’s surface) while there is no upward limit (Seewald, 1998). Another way to define the markedness of words is the relative word frequency in a language (distributional markedness, see e.g. Cho & Proctor, 2007). In the Leipzig Corpora Collection (Quasthoff et al., 2006, the 2011

German corpus) the word “oben” (“up”) appears twice as much as the word “unten” (“down”). This fact leads to the assumption of a markedness of “down” and an unmarkedness of “up”, too. Furthermore, “up” (just like “right”) could be considered as [+] polar, while “down” could be considered as [–] polar (Winter et al., 2015). Hence, the polarity correspondence principle was (in this case) in line with the markedness-account.

Taking this classification for granted, the MARC effect should have occurred in my second study not only along the horizontal, but also along the vertical axis. The same pattern as expected for horizontal axis would have been proposed here. Above all, on the *Diagonal_1:30* an even stronger MARC effect should have been present, since in this axis all three categories were congruent (“right-up-even” vs. “left-down-odd”). Yet, I did not find any of these postulated effects.

One could argue that the above mentioned classification was incorrect. This could be true for two reasons. First, different from what I have proposed above, it could be the case that “up” is marked and “down” is unmarked. In such a case, a strong MARC effect on the other diagonal *Diagonal_4:30* and a reversed MARC effect on the vertical axis should have been present, which was not the case, though. Second, there might be no significant differences in terms of markedness between “up” and “down” at all. In such a case, no MARC effect in vertical orientation would have been expected, but in the diagonal orientation the markedness of “left” vs. “right” should have “taken over” leading to a MARC effect just like in the horizontal condition on both diagonal axes, which, again, was not the case.

Recently the MARC effect was found to be reversed for left-handers (Huber et al., 2015). The authors suggested that the MARC effect would not rely on linguistic markedness, but on *body-specificity*, following the idea that “good” things (or [+] polar) are more associated with the dominant hand (Casasanto, 2009). In contrast to this idea, a robust MARC effect has been reported for verbal answers (Leth-Steensen & Citta, 2016), which would argue against the *body-specific-account* for the MARC effect. Since I did not find a saccadic MARC effect in any of my studies and taking into account the other reported (null) findings (Schwarz & Keus, 2004), it might be that there is no MARC effect for saccadic responses. This result can hardly be explained in "linguistic" terms: why should linguistic effects be different for different effectors? One possibility is that the missing MARC effect in saccadic responses could be explained by the *body-specific-account* resulting in no linguistic effect at all, since no side dominance (like the dominant hand) would be proposed for saccadic eye movements to the left and to the right, despite of the existence of a dominant eye.

4.3 The Mental Number Space

The major aim of my thesis was to investigate the relationship between numbers and space. The world we live in and the space that surrounds us is three-dimensional. Association between numbers and space has been reported for more than one dimension (see Winter et al., 2015 for a review) and my second study points towards the existence of a frontoparallel *mental number plane*. Therefore, the prediction of a *three-dimensional mental number space* might be reasonable, as detailedly described in the following chapters.

4.3.1 Mental Number Space Along the Horizontal Axis

Along with the intensively investigated SNARC effect along the horizontal axis (e.g. Dehaene et al., 1993), a relationship between numbers and the horizontal axis in space has been reported in other studies, too. One example comes from the so-called *random number generation* (RNG) tasks, in which participants were asked to call random numbers while engaged in a spatial task. When doing head movements from left to right and vice versa, numbers were smaller when participants looked to the left-hand side and higher when participants looked to the right-hand side (Loetscher et al., 2008; Winter & Matlock, 2013). Furthermore, a leftward gaze position change resulted the in naming of smaller numbers (compared to the previous trial) and a rightward gaze position change resulted in the naming of larger numbers (Loetscher et al., 2010). All these examples provide evidence for a relationship between numbers and the horizontal axis of space.

4.3.2 Mental Number Space Along the Vertical Axis

In the vertical dimension, the SNARC effect has been reported for bimanual responses (Hartmann et al., 2014) and saccadic eye movements (Schwarz & Keus, 2004). In both cases, larger numbers were associated with the top and smaller numbers were associated with the bottom, just like levels in a skyscraper. This vertical SNARC effect might be weaker or less pronounced than the horizontal SNARC effect (see Winter et al., 2015 for a review) and was not found in other studies with a bimanual task (Holmes & Lourenco, 2012). Holmes and Lourenco even suggested that there might be no "real" vertical SNARC effect and any effects on the vertical dimension would result from a reorientation (or "trump") of the horizontal SNARC effect.

The results from my second study are clearly not in line with this latter point of view and rather suggest the existence of a frontoparallel mental number plane, as proposed by Schwarz and Keus (2004). However, apart from the SNARC effect, other studies reported a relationship between numbers and space in the vertical dimension, too. RNG with vertical head movements (Winter & Matlock, 2013) and vertical eye movements (Loetscher et al., 2010) resulted in larger numbers for upward positions and smaller numbers for downward positions. Movement in an elevator enhanced the response speed to additions during upward movements and subtractions during downward movements (Lugli et al., 2013).

4.3.3 Mental Number Space Along the Sagittal Axis

The SNARC effect along the sagittal axis has been demonstrated for bimanual responses (Ito & Hatta, 2004; Gevers et al., 2006b; Shaki & Fischer, 2012; Chen et al., 2015) and an association of small numbers and near responses as well as large numbers and far responses has been found. In contrast to this orientation, RNG during simulated self-motion with optic flow patterns on the sagittal axis revealed an association of forward motion and small numbers as well as backward motion and large numbers (Seno et al., 2012). Chen and colleagues (2015) additionally investigated the SNARC effect with responses in front and behind the participant. Interestingly, no SNARC effect was present in this experimental arrangement, leading the authors to suggest the SNARC effect in sagittal dimension to be "*isotropic*", i.e. present in terms of *near* and *far* but not in terms of *in front* and *behind*.

4.3.4 Three-Dimensional Mental Number Space

In a third experimental paradigm, Chen and colleagues (2015) tested the SNARC effect on the transverse plane right and left from the sagittal axis. They found evidence for a transverse SNARC plane and proposed an isotropic *mental number space*, e.g. "*a sphere around body with near-small and far-large association"* (Chen et al. 2015, p. 1527). In my second study I found evidence for the existence of a frontoparallel mental number plane, by employing the strength of the SNARC effect along the two cardinal axes to correctly predict the strength of the SNARC effect along the two diagonal axes. These results are fully in line with the proposed *mental number s*pace (Winter et al., 2015). Nevertheless, my results do not support the idea of an <u>isotropic</u> mental number space (like the suggested sphere) where all dimensions are mapped in terms of *far* vs. *near*, since neither the SNARC effect on the horizontal axis (first and second study) nor the SNARC effect along the vertical axis and the diagonal axes (second study) behaved in an isotropic manner. Hence, this *mental number space* might rather be represented by a three-dimensional Cartesian coordinate system. This Cartesian coordinate system could either be described in gaze centred coordinates (sagittal axis along gaze direction) or in body centred coordinates (sagittal axis starting orthogonal on the chest).

4.3.5 Functional Coupling of Eye Movements and Numbers

In addition to the SNARC effect (Dehaene et al., 1993), as reported in my first and second study, another link between numbers and space has been reported: similar to space (Ross et al., 1997; Klingenhoefer & Bremmer, 2009) and time (Yarrow et al., 2001; Knöll et al., 2013) the perceived amount of numbers was compressed by saccadic eye movements (Burr et al., 2010a; Binda et al., 2011) leading to an underestimation of numerosity. Additionally, the results of rapidly computed arithmetical calculations, based on abstract quantities, presented as symbolic numerical magnitude, were compressed during saccades (Binda et al., 2012).

It would be interesting to test, whether number perception is modulated by other non-saccadic eye movements too. For instance, it is known that visual and auditory stimuli are mislocalized not only during saccades (e.g. Ross et al., 2001; Klingenhoefer & Bremmer, 2009), but also during optokinetic nystagmus (e.g. Kaminiarz et al., 2007; Königs et al., 2007) and during smooth pursuit eye movements (e.g. Blanke et al., 2010; Königs & Bremmer, 2010). The mislocalization during saccades can in some cases be described as compression (compression of perceived stimuli to one point in space) and in other cases as shift (shift of perceived stimuli in one direction of the space) (Morrone et al., 1997; Cai et al., 1997; Lappe et al., 2000). A prediction for "shift-like" misperception of numbers might be, according to the frontoparallel mental number plane, that rightward or upward shifts induce an overestimation of number while leftward or downward shifts induce an underestimation of number. As the experiments performed by Burr and colleagues (2010a) and Binda and colleagues (2011) were executed in an illuminated room (with spatial references), a compression of perceived stimuli during saccades could be expected. In contrast to that Binda, Morrone and Bremmer (2012) did not find differences between saccade directions or between additions and subtractions, although a saccadic shift should have been induced by their experimental settings. Hence, it might be possible that misperception of numbers does (merely) occur as compression and not "shift-like". An experiment potentially resulting in interesting findings might be number perception during smooth pursuit on the diagonal axes, since the frontoparallel mental number plane, found in my second study, would predict a strong effect on the one diagonal (Diagonal_1:30), but no or only a weak effect on the other diagonal (Diagonal_4:30). Such an experiment might provide further evidence for the concept of a three-dimensional *mental number space*.

4.4 Implications on Human Number Perception

I investigated different aspects of the processing of numerical information in the context of visual perception. While the first two studies examined different aspects of the SNARC effect, which is based on abstract numbers, represented in the *approximate number system* (ANS), the third study investigated the processing of small visual magnitudes by the *object tracking system* (OTS) and the ANS. In this third study I could find some evidence that in this behavioural context the processing of small magnitudes in the subitizing range might be pre-attentive, i.e. small visual magnitudes might be processed without the need of paying attention. Recent studies (Anobile et al., 2016) argued that all numbers (from one up to “a lot”) are processed by the ANS, but that the OTS additionally supports the perception of magnitudes in the lower range (up to four). This has especially been demonstrated by the attention-dependency of number perception in the subitizing range, which was affected by high attentional load tasks (Anobile et al., 2012). Since participants in my experiment were not instructed to attend to the presented magnitude and hence did not report the processed number, discrimination between the ANS and the OTS in my experiment is hardly accomplishable. Therefore, the observed *mismatch negativity* (MMN) might reflect pre-attentiveness of the ANS or of the OTS. However, the results of my experiment provide evidence for the idea that numbers in this low (subitizing) number range are processed pre-attentively, no matter which of the two systems are involved.

With my first two studies, mainly two findings were validated. Firstly, the SNARC effect depends – in addition to the number representation (e.g. the *mental number line* or the *polarity correspondence principle*) – on number unrelated effects, such as the sensory modality or the effector. Secondly, I could show that for different sensory modalities – at least for saccadic responses – the human brain represents numbers not only on a *mental number line* (Dehaene et al., 1993), but even on a frontoparallel *mental number plane*. This finding is perfectly in line with the predictions of Schwarz and Keus (2004) and the finding of a SNARC effect in the transversal plane (Chen et al., 2015). Taken together, these findings suggest the existence of a three-dimensional *mental number space*, where small numbers are represented *left / down / near* and large numbers are represented *right / up / far*.

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6 Appendix

6.1 Appendix A1 – Study I:

I used catch trials to encourage people to start their response only after having decided on the side to respond to. In these catch trials, I presented non-number words, that were matched in word frequency class with the number words, using the German 2010 corpus from the Leipzig Corpora database (Quasthoff et al., 2006). Word frequency class relates a word's frequency to that of the most common word in the language. For example, "zwei" (two) has a word frequency class of 5, meaning that "der" (the) occurs 2^5 times as often as "zwei". Table 6-1 lists the word frequency class of the number words. Table 6-2 lists the distractor words, sorted by their frequency class. The number in brackets indicates the total amount of used words in frequency class.

Table 6-1: The word frequency classes of the number words used in the experiment.

German number word	Word frequency class	English translation
eins	9	one
zwei	5	two
drei	5	three
vier	6	four
sechs	6	six
sieben	7	seven
acht	7	eight
neun	8	nine

Table 6-2: Distractor words, grouped by word frequency class.

German	*English*	German	*English*	German	*English*	German	*English*
Frequency 5 (38)		Frequency 6 (38)		Frequency 7 (38)		Frequency 8 (21)	
ab	*off / from*	andere	*different / other*	Anfang	start / beginning	Bild	*picture / image*
alle	*all*	dabei	*alltough /*	Arbeit	work / job	Buch	*book*

			thereby						
beim	*during*	denn	*because*	Art	kind / type	Film	*film*
bereits	*already*	dieses	*this*	dabei	although / thereby	Firma	*company*
damit	*thereby*	etwa	*about / for example*	dagegen	in contrast / against	Form	*shape / form*
dann	*then*	etwas	*any / some*	damit	so that	Hand	*hand*
dieser	*this*	Fall	*drop / case*	daran	at it	Herr	*sir / lord*
Ende	*end*	Frau	*woman /wife*	Eltern	parents	Lage	*layer / position*
geht	*walks*	gut	*good*	Entwicklung	development / evolution	Mensch	*human / man*
gibt	*gives*	heute	*today*	Ergebnis	result / sum	Musik	*music*
hatten	*had*	ihm	*him*	Familie	family	Opfer	*casualty / victim / sacrifice*
ihre	*her / their*	jedoch	*but / however*	Frage	question / demand	Problem	*trouble / problem*
immer	*always / forever*	Kinder	*children / infants*	Geld	money / cash	Programm	*program / agenda*
Jahr	*year*	Land	*country / land*	Grund	reason / ground	Projekt	*project*
jetzt	*now*	lassen	*let / allow*	hinter	after / behind	Rang	*grade / rank*
kann	*can / may*	Leben	*life / lifetime*	jeder	any / each / everybody	Schule	*school*
können	*can / may*	machen	*do / make*	knapp	narrow / tight	Stück	*piece / play / slice*
Menschen	*people / humans*	Mann	*man / husband*	Kosten	costs	Titel	*title*
muss	*must*	ob	*if / whether*	Kunden	customers	Verfügung	*order / directive*
müssen	*have to*	Platz	*place / spot / plaza*	Leute	people / folks	Wasser	*water*
neue	*new / another*	Regierung	*government*	Männer	man / guys	Wirtschaft	*economy*
nun	*now / well*	seinem	*his*	möglich	possible	Frequency 9 (21)	
rund	*round*	selbst	*even /self*	nie	never / at no time	Antwort	*answer / reply*
sagt	*says*	sogar	*even /*	Partei	party	Auge	*eye*

			actually				
schon	*already / yet*	sollen	*shall*	Politik	politics	Betrieb	*business*
seine	*his*	sondern	*but / assort*	Präsident	president	Blatt	*sheet / leaf*
seit	*for / since*	sowie	*plus / as soon as*	Rolle	part / role	Brief	*letter*
soll	*should / quota*	Stadt	*city / town*	Seite	page / side	Büro	*bureau / office*
unter	*under / below*	steht	*stands / suits*	Spiel	game / match /act / play	Erde	*earth / ground*
vom	*from*	Uhr	*clock / watch*	Sprecher	speaker	Feld	*field / domain*
waren	*were / goods*	uns	*us / ourselves*	statt	instead of	Fenster	*window*
weiter	*along / in addition*	Unternehmen	*corporation / organisation*	Teil	part / fraction	Hotel	*hotel*
wenn	*if / when*	wegen	*because of / due to*	Thema	issue / matter	Kunst	*art / skill*
werde	*become*	weil	*because / since*	Trainer	manager / trainer	Macht	*power / force / might*
wieder	*again*	Welt	*world*	Zahl	number / digit	Netz	*net / web*
wir	*we*	Woche	*week*	Ziel	aim / goal	Papier	*paper*
wurden	*become*	wollen	*desire / will / want*	Zukunft	future	Plan	*plan / map / program*
zwischen	*among / between*	Zeit	*time*	zusammen	together / in all	Satz	*phrase / sentence*
						Sonne	*sun*
						Tat	*act*
						Tisch	*table / desk*
						Trend	*trend / movement*
						Tür	*door*

6.2 Appendix A2 – Study I:

Table 6-3: Mean reaction times [ms] to the right and to the left for each number, averaged across all participants as well as reaction time differences (right – left) [ms].

effector	response side	1	2	3	4	6	7	8	9
Finger	right	661	680	711	626	624	661	605	665
	left	621	679	685	628	649	636	628	644
	right – left	40	1	26	–2	–25	25	–23	21
Eye	right	573	574	588	535	552	547	535	546
	left	554	565	595	536	557	545	545	563
	right – left	19	9	–7	–1	–5	2	–10	–17
Arm	right	564	574	612	540	546	558	527	572
	left	567	606	610	560	582	568	553	571
	right – left	–3	–32	2	–20	–36	–10	–26	1

6.3 Appendix B1 – Study II:

Table 6-4: Averaged reaction times [ms] separated for modalities (auditory and visual), orientations (R–L, U–D, RU–LD and RD–LU) and response side (R (right), L (left), U (up), D (down), RU (rightup), LD (leftdown), RD (rightdown) and LU (leftup)) for each number. The difference in reaction time between the two corresponding response sides is given below the reaction times of these sides (R–L, U–D, RU–LD and RD–LU).

			1	2	3	4	6	7	8	9	mean
auditory	R–L	R	546,7	518,2	515,0	531,5	540,8	558,0	517,9	522,4	531,3
		L	528,7	537,5	518,0	545,7	562,9	540,7	535,4	516,6	535,7
		R–L	18,0	–19,3	–3,0	–14,2	–22,2	17,3	–17,5	5,8	–4,4
	U–D	U	546,9	539,8	521,4	543,9	562,8	548,7	533,4	526,0	540,4
		D	557,7	543,4	533,0	555,9	578,9	570,5	547,1	541,7	553,5
		U–D	–10,7	–3,6	–11,6	–12,0	–16,1	–21,8	–13,6	–15,7	–13,1
	RU–LD	RU	551,8	518,3	520,8	531,7	545,7	544,4	515,4	524,8	531,6
		LD	537,6	546,1	526,4	554,7	568,6	549,4	549,5	527,6	545,0
		RU–LD	14,2	–27,7	–5,6	–23,0	–22,9	–4,9	–34,0	–2,8	–13,4
	RD–LU	RD	528,4	509,6	505,7	532,0	541,5	540,9	511,9	516,8	523,3
		LU	518,4	526,8	503,9	528,9	552,5	527,7	515,5	506,6	522,5
		RD–LU	9,9	–17,2	1,8	3,1	–11,0	13,1	–3,6	10,3	0,8
visual	R–L	R	383,3	385,5	389,2	385,1	388,4	386,9	379,8	387,8	385,8
		L	382,6	389,6	399,5	384,7	404,1	383,2	396,0	408,6	393,5
		R–L	0,7	–4,2	–10,3	0,4	–15,6	3,7	–16,2	–20,8	–7,8
	U–D	U	380,8	394,4	394,9	385,5	395,9	379,7	392,5	396,9	390,1
		D	395,6	389,5	404,0	394,8	414,3	391,1	401,6	407,9	399,8
		U–D	–14,8	4,9	–9,1	–9,3	–18,4	–11,4	–9,1	–11,0	–9,8
	RU–LD	RU	386,8	387,7	387,1	378,8	391,9	384,8	378,4	388,9	385,6
		LD	380,7	382,5	398,2	386,7	405,1	388,0	397,8	412,4	393,9
		RU–LD	6,1	5,2	–11,1	–7,9	–13,2	–3,2	–19,4	–23,6	–8,4
	RD–LU	RD	383,7	384,6	390,2	381,9	401,4	385,4	392,9	391,6	389,0
		LU	377,3	383,5	392,3	376,8	395,6	379,0	391,7	396,0	386,5
		RD–LU	6,4	1,1	–2,2	5,1	5,8	6,4	1,2	–4,3	2,4

6.4 Appendix B2 – Study II:

Table 6-5: Results of repeated measures ANOVA with factors magnitude (ma: 1 & 2 / 3 & 4 / 6 & 7 / 8 & 9), response side (rs: "large numbers preferred side" / "small numbers preferred side") and parity (pa: even / odd). The SNARC effect is indicated by a significant interaction *magnitude* x *response side*, while the MARC effect is indicated by a significant interaction *response side* x *parity*. ANOVAs were performed individually for sensory modality, axis, RT- and ER-conditions.

		axis	ma	rs	pa	ma x rs	ma x pa	rs x pa	ma x rs x pa
RT	auditory	R – L	***	n.s.	.040	n.s.	***	.078	n.s.
		U – D	***	**	**	n.s.	***	n.s.	n.s.
		RU – LD	***	***	.018	n.s.	***	n.s.	.064
		RD – LU	***	n.s.	**	n.s.	***	n.s.	n.s.
	visual	R – L	**	.024	n.s.	.056	***	n.s.	.011
		U – D	.039	.028	n.s.	n.s.	***	n.s.	n.s.
		RU – LD	***	.043	.069	***	**	n.s.	**
		RD – LU	***	n.s.	n.s.	n.s.	***	n.s.	n.s.
ER	auditory	R – L	***	.098	n.s.	n.s.	***	n.s.	n.s.
		U – D	***	n.s.	n.s.	n.s.	***	n.s.	n.s.
		RU – LD	***	n.s.	n.s.	***	**	n.s.	n.s.
		RD – LU	***	n.s.	n.s.	n.s.	***	n.s.	.011
	visual	R – L	***	n.s.	n.s.	.048	n.s.	n.s.	n.s.
		U – D	***	n.s.	n.s.	**	.039	n.s.	n.s.
		RU – LD	***	n.s.	.054	***	.026	n.s.	.024
		RD – LU	.023	n.s.	n.s.	n.s.	.017	n.s.	.051

7 Declaration of Authors’ Contributions to the Studies

This thesis consists of three studies I first authored, which are partly published in peer-reviewed journals or are currently prepared for publication.

Study I / Chapter 3.4:

Philipp N. Hesse, Katja Fiehler & Frank Bremmer (2016)

SNARC Effect in Different Effectors

Perception, 45(1-2), 180-195.

The study was planned by **Philipp N. Hesse**, Dr. B. Marius ’t Hart, Prof. Dr. Katja Fiehler and Prof. Dr. Frank Bremmer. The experiment was designed and programmed by **Philipp N. Hesse**. Data were collected and analysed by **Philipp N. Hesse**. The manuscript for the publication was written by **Philipp N. Hesse** and proofread by Dr. B. Marius ’t Hart, Prof. Dr. Katja Fiehler and Prof. Dr. Frank Bremmer. The chapter in this thesis based on the manuscript was written by **Philipp N. Hesse**.

Study II / Chapter 3.5:

Philipp N. Hesse & Frank Bremmer (in preparation)

The SNARC Effect in Two Dimensions:
Evidence for a Mental Number Plane

The study was planned by **Philipp N. Hesse** and Prof. Dr. Frank Bremmer. The experiment was designed and programmed by **Philipp N. Hesse**. Prof. Dr. Katja Fiehler provided the auditory stimuli. 20% of the data were collected by student research assistant Steven

Youngkin under supervision by **Philipp N. Hesse**. 80% of the data were collected by **Philipp N. Hesse**. Data were analysed and the chapter was written by **Philipp N. Hesse**.

Study III / Chapter 3.6:

Philipp N. Hesse, Steffen Klingenhöfer & Frank Bremmer (in preparation)

Pre-Attentive Processing of Numerical Visual Information

The study was planned by **Philipp N. Hesse**, Dr. Steffen Klingenhöfer and Prof. Dr. Frank Bremmer. The experiment was designed and programmed by **Philipp N. Hesse**. 22% of the data were collected by student research assistant Natalie Heyse and 10% by Constanze Schmitt both under supervision by **Philipp N. Hesse**. 68% of the data were collected by **Philipp N. Hesse**. Data were analysed and the chapter was written by **Philipp N. Hesse**.

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